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Tanypleuridae fam.nov. (Copepoda: Caligoida), Parasitic on Fishes in the Canadian Atlantic

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The discovery, in Canadian Atlantic waters, of *Tanypleurus alcicornis* Steenstrup and Lütken, 1861, is reported. This is the first find of the species since its description. Its morphology, including the structure of appendages, is examined. A new family Tanypleuridae is proposed.

Received December 13, 1968

Sir William Hardy, the research ship of the Torry Research Station in Aberdeen, Scotland, worked in Newfoundland waters in April 1967. On April 19, in the position 47°20′N, 52°00′W, the catch, taken at a depth between 85 and 90 fath, included three specimens, all about 30 cm long, of *Lycodes reticulatus* Reinhardt. Attached to the gills of one of these fish was a specimen of a parasitic copepod which, in due course, was placed at my disposal. The specimen was readily identifiable as *Tanypleurus* species (Steenstrup and Lütken, 1861).

The finding of this specimen amounts to a rediscovery of the genus *Tanypleurus*, seen on only two previous occasions, both over a hundred years ago and both reported on in the same paper (Steenstrup and Lütken, 1861). These authors examined and described, under the name *T. alcicornis*, two specimens from the gills of *Cyclopterus spinosus* Müller (=*Eumicrotremus spinosus*), taken in Greenland waters. Two further specimens were found in the same region in the stomach of the Greenland shark *Somniosus microcephalus* (Bloch and Schneider). It was presumed that they were swallowed by the shark with another specimen of *E. spinosus* which had been digested by the time of the shark's capture.

No further records followed and *Tanypleurus* attracted but scanty attention from copepod specialists. Comments made on it subsequently differed widely in assessment of its proper place among the parasitic copepods.

The find of this single specimen afforded an excellent opportunity for reexamining the genus, with a view to settling the doubts as to its affinities. Its appendages had to be dissected and examined in detail, even if this involved the destruction of the specimen. It was also necessary to compare it with the original specimens, since Steenstrup and Lütken's (1861) figures seemed to suggest the existence of several differences between them and the recent find. Thanks to the good offices of Dr Torben Wolff from the University of Copenhagen, Denmark, four original specimens were made available for comparison. One of them was selected as the lectotype of the species.

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As a result of this study, I arrived at the conclusion that *Tanypleurus* should be placed in a new family. This paper describes the morphology of *T. alcicornis* and discusses the reasons for my conclusion as to its taxonomic position. The following description is based on the new specimen, unless otherwise indicated.

Tanypleurus alcicornis Steenstrup and Lütken, 1861

General Appearance (Fig. 1 and 2)

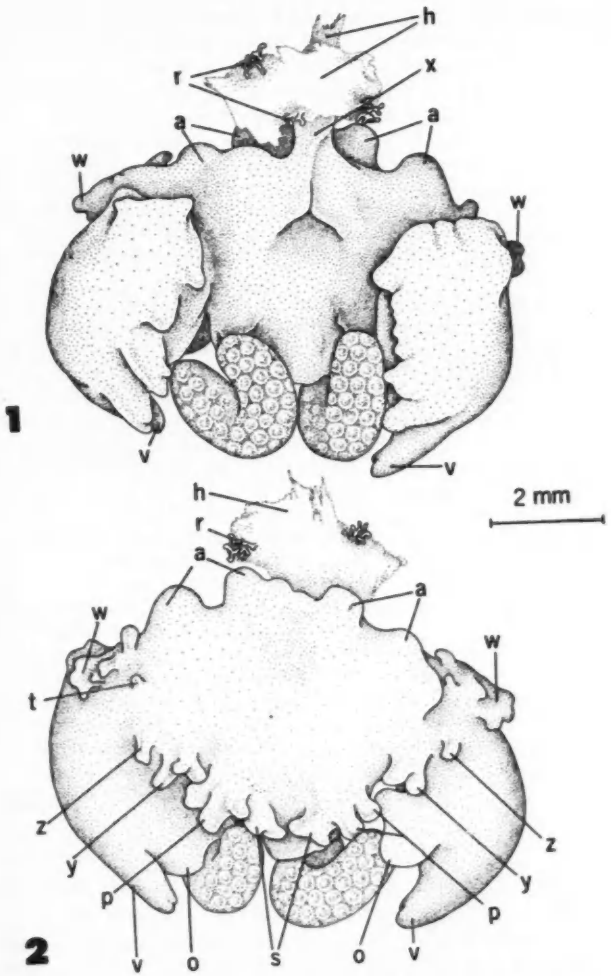
The shape of this parasite is very complicated. The two parts immediately obvious to the observer are the trunk and the egg sacs. The trunk is wider than long (9.71 × 4.32 mm) and curves ventrally on both lateral margins (Fig. 1). The curving parts form aliform expansions, posteriorly separated from the central part by deep clefts (Fig. 2). The trunk, therefore, is divisible into a central and two lateral parts, not demarcated along the anterior margin. The lateral margins of the trunk (which are topographically ventral due to the curving of the "wings") are divided into several lobes. In front of the posterior digitiform lobe of the right wing (*v*, Fig. 1) there are four lobes along the ventral margin. The left wing did not have all these lobes normally formed, but comparison with the original specimens (Fig. 11) suggests that four ventral lobes is a regular feature of the species. On the dorsal surface of the wing, yet another lobe (*o*, Fig. 2) projects in a medial direction. The dorsal surface of the anterior part of the wing carries one more prominent extension (*w*, Fig. 1 and 2) which consists of several apparently irregular swellings and tubercles. Near the extension *w*, on the left wing of the specimen, there was also a small tubercle (*t*, Fig. 2). Comparison with the type material (Fig. 12) shows that it is normal for both wings to have this tubercle.

The dorsal and ventral surfaces of the central part of the trunk are more or less smooth, but its posterodorsal margins are fringed by a series of outgrowths which, in spite of their variability, seem to form a definite pattern. Nearest to the posterior extremity and almost touching each other above its surface are two processes, in this specimen slightly bifid (*s*, Fig. 2). Next in line is a group of processes which, on the left side, consists of three digitiform outgrowths arising from a single peduncle and, on the right, of two similar but more or less separate outgrowths (*p*, Fig. 2). Anterolateral to *p* are two more structures (*y* and *z*, Fig. 2). The former consists of two processes on the right and three on the left, whereas the latter is a single blunt outgrowth on each side.

The posterior extremity (Fig. 3) tapers to a rounded tip. In dorsal view only a part of the anal slit can be seen. The ventral view, however, shows that the tip is subdivided, three lobes being discernible on each side of the midventral line. The most lateral of these accommodates the orifice of the oviduct, seen as an oblique slit reinforced by a bar of thick cuticle. From the orifice emerges the egg sac (*e*), multiserial and curling in a dorsal direction. A distinct groove divides the lateral from the central lobe. The medial borders of the two central lobes run obliquely inwards and upwards. At the point of their meeting a small conical tubercle projects above the surface. This is the genital process (*gp*, Fig. 3). The innermost lobes are formed from the abdominal tubercle, divided into two by the anal slit (*an*, Fig. 3). Figure 3 also shows the outlines of the inner lobes of the wings (*o*) and the tips of the dorsolateral structure *p* on the right.

Anteriorly, the central part of the trunk has a transverse margin, bulging in a "dorsal hump" consisting of four swellings, symmetrically arranged on each side (*a*, Fig. 1 and 2). The lateral pair is more ventral than the medial. In the centre of the dorsal hump, just ventral to its base, is a small conical tubercle (*c*, Fig. 5), the cephalothorax. The cone is almost regular in shape and is surmounted by a minute buccal tube (*b*) accompanied by the appendages. Along the dorsal side of the cone can be seen two diverging bands of tissue, the long muscles serving the appendages. Other similar strands of muscle run in a ventral direction from the buccal tube.

The ventral surface of the central part of the trunk is covered anteriorly by the very broad, and almost flat, bases of the second maxillae. These fuse together near their bases, forming a



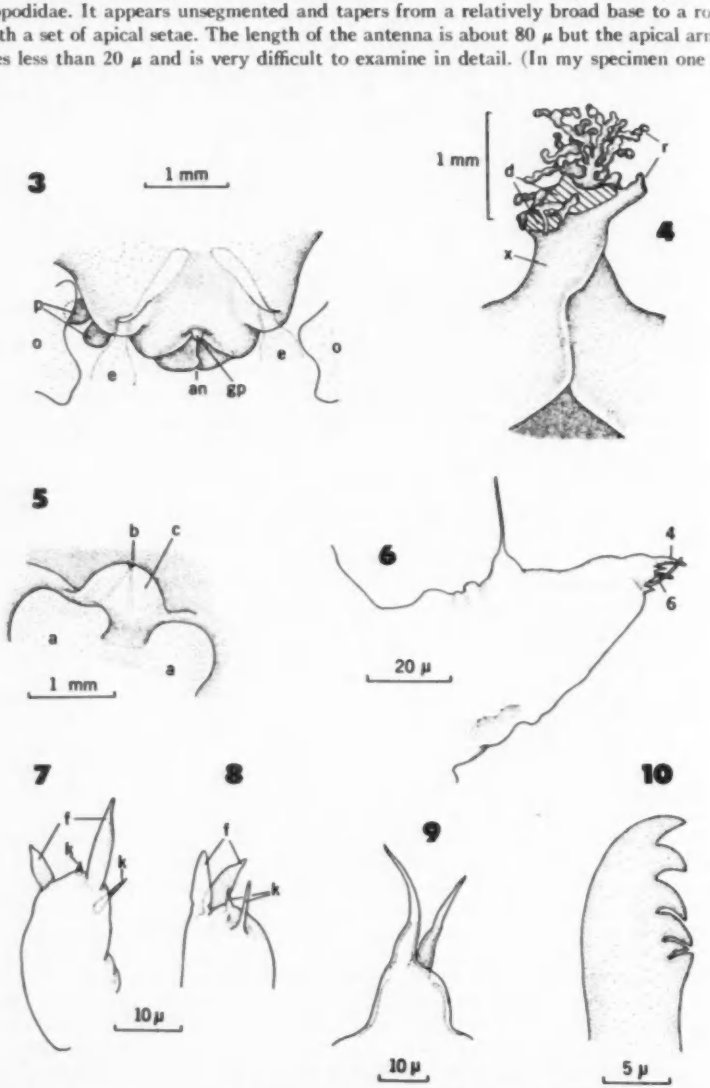
FIGURES 1 and 2. ***Tanypleurus alcicornis,*** female from *Lycodes,* general view.
Fig. 1. Ventral; Fig. 2. Dorsal (lettering in text).

notch like an inverted Y (Fig. 2, 4). The cephalothorax is completely obscured from the ventral side by these appendages and from the dorsal side by the hump. It is not easy to find.

THE APPENDAGES (FIG. 4–10)

Situated at the apex of the cephalothorax, the buccal tube consists of ventral and dorsal components and resembles in general the lernaeopodid mouth. Slight pressure on the lateral side of the tube separates the two components along the usual slit between them and permits one to observe the tips of the emerging mandibles.

The first antenna (Fig. 6) bears a general resemblance to the corresponding appendage in Lernaeopodidae. It appears unsegmented and tapers from a relatively broad base to a rounded apex with a set of apical setae. The length of the antenna is about 80 μ but the apical armature measures less than 20 μ and is very difficult to examine in detail. (In my specimen one of the



FIGURES 3–10. ***Tanypleurus alcicornis,*** female from *Lycodes*, details.

Fig. 3. Posterior extremity, ventral; Fig. 4. Second maxillae, ventral; Fig. 5. Mouth cone, anterodorsal; Fig. 6. First antenna, lateral; Fig. 7. Second antenna, entire, dorsolateral; Fig. 8. Same, distal half, ventral; Fig. 9. First maxilla, ventromedial; Fig. 10. Mandible, tip, nearly lateral. (*an* = anus; *b* = position of buccal tube; *c* = cephalothorax; *d* = damaged area; *e* = egg sac; *gp* = genital process; *r* = rootlets of holdfast; *x* = stalk of second maxillae; other lettering in text.)

first antennae was missing, so that all the observations made on this appendage must be only tentative and subject to amendment, when more data become available.) The apical armature consists of five structures, at least two of which by their shape and position suggest homology with similar structures in Lernaeopodidae. These are seta 4 (Fig. 6) on the medial side of the apex and seta 6 on the lateral side of the apex. The numbers were given in accordance with my practice adopted for lernaeopodid setae of the first antenna (Kabata, 1964). There are also two shorter setae, one sharp and one blunt, as well as a pointed tubercle at the base of seta 6. At about midlength the antenna carries on its dorsomedial side a pronounced swelling, from the tip of which arises a long seta. The outstanding characteristic of the first antenna of *Tanypleurus* is its size. In Lernaeopodidae, which have similar first antennae, it is about the smallest of all appendages. In *Tanypleurus* it is the largest appendage around the buccal tube, being equal to the latter in length.

The second antenna (Fig. 7 and 8) is quite unlike that of any known family in the order Caligoida. It appears uniramous. Its stout, fairly short body with rounded tip is surmounted by four structures. These are of two kinds: there are two long and robust tapering outgrowths (*f*, Fig. 7 and 8) and two setiform ones, shorter and slender (*k*, Fig. 7 and 8). One of the former two is longer than the other and situated on the dorsal side of the apex, the other is on the ventral side. The two setiform outgrowths are also unequal in size, the longer being nearer the ventral side of the apex, the shorter almost exactly apical.

The mandible (Fig. 10) is also reminiscent of many caligoid mandibles. It is a short, blade-like structure, only about 45 μ long. The serrated margin of its tip carries a series of five teeth, more or less uniform in size, except for the smaller basal tooth. (It is possible that Fig. 10 does not show the true shape of the teeth. The distal tooth, which appears rather upturned, suggests that the appendage was not viewed in a strictly lateral plane. Any displacement from this plane often distorts the appearance of the teeth.)

The first maxilla (Fig. 9) is a small tubercle tipped with two setae which have slightly inflated bases. No additional details were observed.

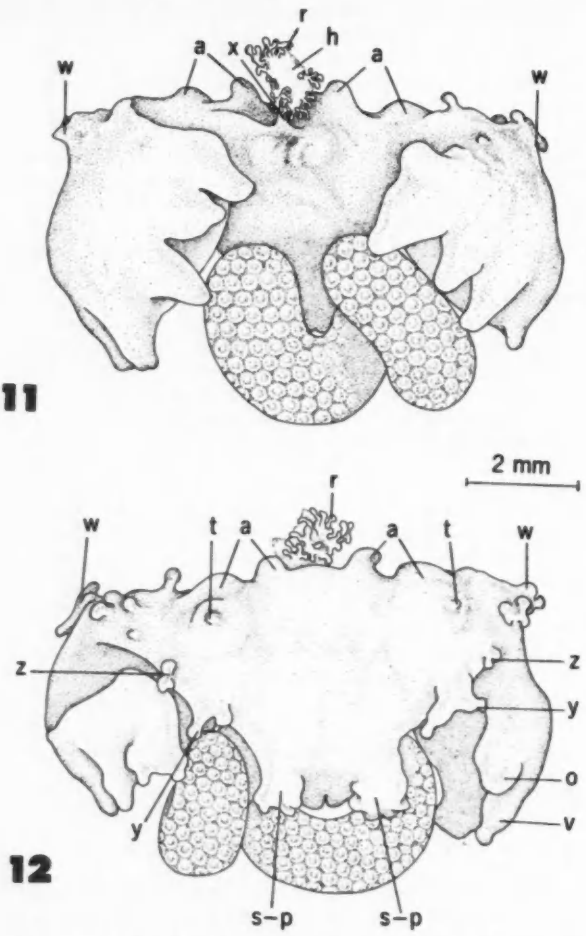
The second maxilla (Fig. 4) forms the attachment organ. The two appendages are flat at their bases but after fusing they form a short stalk, circular in cross-section. The line of fusion is clearly discernible throughout the major part of the stalk. The stalk breaks up distally into a maze of dendritic rootlets, very fine and intimately entangled with the surrounding tissues of the host. The entire holdfast is so delicate that it is not possible to extricate it without damage. In Fig. 4 the damaged areas (*d*) are diagonally striped.

The maxilliped is absent.

DISCUSSION

The first task of this study was the identification of the specimen by comparing it with the original ones described by Steenstrup and Lütken (1861). The two specimens from *Eumicrotremus spinosus* were similar in size to mine (7.65 × 4.25 mm and 9.53 × 5.10 mm). One of the specimens removed from the stomach of the shark was dismembered, but the other was distinctly larger (14.11 × 7.65 mm).

Unable to dissect the Danish specimens, I had to restrict my comparison to larger morphological features, particularly to the structure of the trunk. The lectotype of *Tanypleurus alcicornis* is shown in Fig. 11 and 12. Although it differs in some respects from the Canadian specimen, the underlying similarity is undeniable. On the dorsolateral margins of the central part of the trunk, the lectotype has a series of processes which are about the same as in the Canadian specimen, though processes *s* and *p* are fused (*s-p*, Fig. 12). The process *z* is not single but distinctly bifid. Another important difference is



FIGURES 11 and 12. ***Tanypleurus alcicornis***, lectotype, general view.
Fig. 11. Ventral; Fig. 12. Dorsal (lettering in text).

the size and thickness of the stalk formed by the second maxillae (*x*, Fig. 11). In the lectotype this stalk is much more slender and smaller. The four lobes of the lateral margins of the wings are equally developed. As seen in dorsal view (Fig. 12) the left wing of the lectotype is crumpled. The right wing, however, has the slightly indented lobe *o* and the typical lobe *v*, as in the Canadian specimen.

In my earlier study of the genus *Nicothoe* (cf. Kabata, 1967), I attempted to show that the parasitic copepods with complicated trunk structure exhibit

a good measure of variability, depending on the conditions prevailing at their site of attachment and the identity of the host. Some parts of the trunk may become overdeveloped, others underdeveloped. Certain outgrowths and protrusions might be suppressed, others might change their shapes. On occasion some spurious processes make their appearance. In spite of these differences, however, the basic pattern of the species is unmistakable. Comparison of Fig. 1 and 2 with Fig. 11 and 12 suffices to demonstrate the existence of such a specific pattern and convincingly proves that the specimen taken from *Lycodes* in 1967 is conspecific with those described from *Eumicrotremus* in 1861. The difference in size of the attachment organ may be attributed to the difference in hosts.

The discoverers of *Tanypleurus alcicornis* did not study the appendages of the species. The description shows, however, that Steenstrup and Lütken (1861) understood the morphology of this parasite. Without expressing any views on the taxonomic position of *Tanypleurus*, they recognized that the attachment organ of this parasite is "a shortened pair of arms or maxillipeds, similar to those found in *Lernaeopoda* or *Anchorella*." It is clear that very few, if any, subsequent investigators took the trouble to read the old Danish text of the original description. The only one who suggested that the affinities of *Tanypleurus* lie with Lernaeopodidae was Wilson (1920). Without examining specimens, however, he could make only a tentative suggestion. On the other hand, Bassett-Smith (1899), without giving reasons for his decision, placed *Tanypleurus* in the family Chondracanthidae, out of the order Caligoida. Hansen (1923) also attached *Tanypleurus* to the end of his account of Chondracanthidae, stating that his taxonomic diagnosis was only tentative. Yamaguti (1963) placed it quite firmly in Chondracanthidae, stating in his generic diagnosis that *Tanypleurus* had a "head small, rounded, covered with a number of papilliform processes." Thus, the second maxillae were mistaken for the "head," doubtless by analogy with such chondracanthid genera as *Trichthacerus* Krøyer, 1863 and *Triphyllacanthus* Oakley, 1930.

The study of the appendages makes it quite clear that *Tanypleurus* cannot be placed in Chondracanthidae, nor, indeed, in the same order with this family. Its affinities are with Lernaeopodidae in the order Caligoida. The modification of the second maxillae into an attachment organ makes these affinities very strong. With the exception of the very closely related Naobranchiidae, no other family uses its second maxillae in this fashion. Within Lernaeopodidae, the genus *Dendrapta* Kabata, 1964, has a very similar system of rootlets, branching from the second maxillae. In spite of these similarities, however, *Tanypleurus* cannot be included in Lernaeopodidae, because of the following characteristics:

(i) The structure of its second antenna is completely alien to Lernaeopodidae. In fact, it resembles no other second antenna known to me.

(ii) The first maxilla does not resemble that of Lernaeopodidae, but rather that of Lernaeoceridae, otherwise obviously unrelated.

(iii) Very characteristically, the female of *Tanypleurus* possesses no maxillipeds. This is also in contrast to Lernaeopodidae, though not to Lernaeoceridae. Since there cannot be any questions of *Tanypleurus* being a lernaeocerid, it cannot be placed in any known family. I propose, therefore, the establishment of a new family, Tanypleuridae, with the following diagnosis.

Tanypleuridae fam.nov.

Female — Caligoida, Achtheriformes. Cephalothorax reduced to a small conical outgrowth. Mouth parts minute. First antenna of lernaeopodid type. Second antenna apparently uniramous, small, without signs of prehensile adaptation. Mandible of usual caligoid type. First maxilla resembling that of Lernaeoceridae. Second maxilla modified to form attachment organ. Maxilliped absent.

Male — Unknown.

Type genus — *Tanypleurus* Steenstrup and Lütken, 1861.

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The Community Concept in Marine Zoology, with Comments on Continua and Instability in Some Marine Communities: A Review

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The community concept has had a long, complex history in plant and animal ecology. Divergent views about the nature of communities have been most marked in plant ecology: the Zurich–Montpellier school regarded plant communities as largely abstract, based on a mosaic of vegetation, whereas the Uppsala school and other northern plant ecologists regarded communities as concrete, quantifiable units. The analogy between communities and organisms has been used often, particularly in American dynamic ecology, although the analogy can only be a loose one. Communities have also been regarded as abstractions from independent continuous distributions of the individual species. This idea has been used in recent gradient analysis of plant communities.

Similar and equally variant ideas have been used in marine zoology. Many studies in marine ecology have been based on Möbius' concept of the biocoenosis, or on Petersen's use of dominant or conspicuous index species, with added theoretical notions which apparently originated in plant ecology. New evidence is presented that some marine benthic communities may be characterized in terms of dominants while also allowing analysis as parts of continua of distribution along gradients. In addition, although stability usually increases as communities evolve, some types are intrinsically unstable because of the activities of the organisms themselves, rather than because of changes in the physical environment alone.

Because there are different kinds of marine "communities" a single rigorous definition seems impossible. A definition is proposed which avoids theoretical suppositions about community dynamics to allow the variety of phenomena in community relations to be investigated in a relatively unbiased way.

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INTRODUCTION

THERE HAS BEEN MUCH CONTROVERSY through the years over the nature and definition of biotic communities. Much of the difficulty inherent in the community concept arises because many groupings of organisms appear to be more than random assemblages and seem to show some degree of integration, while plant and animal distributions also follow gradients, both real and abstract.

This paper examines community concepts used in marine benthic zoology, explores the role of adaptation to instability in community dynamics, and stresses both the inutility and impossibility of defining *community* rigorously

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because of the diversity of phenomena involved. Part of this discussion is based on an excellent review by Whittaker (1962), containing much of value in examining community concepts used by botanists and zoologists.

Plant ecologists have used three terms which require explanation before further discussion. *Community* has generally come to mean "an ecological unit of any degree" (cf. Macfadyen, 1963) and is thus a broad term, widely applicable. *Formation* means a major grouping of organisms with a definite physiognomy and structure (for example boreal forest, tundra, prairie). *Association* means the units of which formations are composed, that is, groupings of plants in a habitat, marked by unique dominant species or overall composition. (For more detailed definitions of these terms, see Carpenter (1958); Hanson (1962)). The botanical concept of the association comes closest to the community concept of the zoologist. Throughout this paper the ideas underlying the "association" of the plant ecologist, i.e., the "community" of the zoologist, are examined in greatest detail.

HISTORY OF THE COMMUNITY CONCEPT

A brief account of currents in older European plant ecology will indicate the long history of divergent opinion on how natural groups of organisms can be interpreted. Whittaker (1962) reviews the effect of two schools of plant ecology. In central and southern Europe, the Zurich–Montpellier school, greatly influenced by Braun-Blanquet, regarded vegetation as a mosaic, made up of more or less abstract units of various sizes based on "floristic composition," that is lists of species, combined with estimates of the degree of clumping of each species and the area covered by it. Relatively rare "character species" were often diagnostic, since they were found with great "fidelity" in associations, unlike dominant species, which were more widespread. The units could then be grouped together in a hierarchy on the basis of their similarities to each other. In such a taxonomy the lowest category, the association, came to be regarded as analogous to the species. The theory and methods involved have been reviewed by Poore (1955a, b) and an interesting recent example is given by Janssen (1967) who, however, handles the final grouping of data somewhat differently from the Zurich–Montpellier school and arrives at continua of associations as well as a ranking of separate categories.

In northern Europe, the Uppsala school and other Scandinavian plant ecologists also set up a classification of plant ecological units, although their approach was quite different. Associations were regarded as real or concrete, and were based on actual counts of plants (not just estimates of cover or clumping) from small quadrats. Analysis was by simple mathematical methods, for example, the trellis diagram (Macfadyen, 1963), and associations were said to be characterized by dominants or constants (species occurring in all the samples from any association) and to have sharp boundaries. Also entering into the characterization of associations and their grouping into formations were the "life forms" of the plants involved (i.e., their height, and especially the position of the overwintering buds), stressed by Christian Raunkiaer

and the use of dominants, stressed by Eugenius Warming. Like those of the Zurich–Montpellier school, northern European ecologists aimed at classifying vegetation, although the units were regarded as concrete. Other conceptual and methodological differences concerned the size of the units studied, the use of constants or character species, the method of sampling, and the approach to transitions between associations. (For an extended list, see Whittaker (1962)).

As Whittaker (1962) has stressed, these differences of approach and opinion in plant ecology very largely reflect the differences of climate and ecological structure in southern and northern Europe. There also remain psychological and methodological biases, usually unexpressed, which lead some scientists to find continua, and others discrete groups, even when dealing with the same organisms in the same area.

HOLISTIC VIEWS OF COMMUNITIES

The view that ecological units have a development or ontogeny has been especially important in the United States. This idea may have historical origins in the contrast between the relatively untouched continent of the 17th and 18th centuries and the land much modified by agriculture, mining, and industry by the late 19th century. The existence of ecological units ranging from highly disturbed to relatively untouched results naturally in the idea of succession or development of vegetation. Although Raup (1964) has criticized overzealous application of the ideas of climax vegetation and primeval forest in North America, an observer of North American environments can see vegetation (and associated animal groupings) of incredibly different diversity and stability, apparently related to recency of disturbance.

Clements (1916) elaborated the idea of succession and climax. To Clements, the formation is the basic unit of vegetation and formations go through a natural process of development (succession) to a climatically controlled climax, characteristic of the area. The formation (i.e., grouping of related associations in equilibrium with climate) "...is an organic entity," and has an ontogeny and phylogeny, like an organism. Clements' ideas and terminology have been immensely influential: Clementsian phrases and ideas turn up in many contexts, often without the specific content or relevance that Clements intended.

The concept of *organism* has also been developed in a widely used book by Allee et al. (1949), who define a "major community" (equivalent to Clements' formation) as "...a natural assemblage of organisms, which, together with its habitat, has reached a survival level such that it is relatively independent of adjacent assemblages of equal rank; to this extent, given radiant energy, it is self-sustaining." The major community has, by analogy to organisms, anatomy, physiology, and heredity, and also a form of evolution through succession to a stable climax, which is in equilibrium with the environment. These authors say, further, that communities, by their definition, are composed of "...ecologically compatible species populations whose collective ecological requirements of food, shelter and reproduction are satisfied,

in the last analysis, by a certain range of environments." Note that this description does not necessarily mean that communities must have discrete boundaries. Indeed, Allee et al. (1949) admit that aggregations of various degrees of discreteness exist: "....it should be reemphasized that, within the concept of the relatively independent major community at the level of survival for interdependent populations, there is an almost infinite series of biocoenoses, and ecological assemblages of diverse rank, extent, and complexity." Apart from this weakening of the concept of "major communities," the main disadvantage of the approach taken by Allee et al. is that the existence of communities is assumed. There is no attempt to marshall evidence, particularly for the organismic nature of major communities.

Tansley (1920) examined Clements' idea of organism, and although he concluded that real vegetational units exist (as opposed to abstract groupings) he felt that the analogy with organisms could not be maintained because: (1) individuals of the plant community are autonomous in growth, feeding, and reproduction, whereas the cells of an organism ordinarily are not; (2) there is no central control (for example, a central nervous system or genetic apparatus as in true organisms) on which the integration or development of the community is based.

The community, however, is a *quasi-organism* according to Tansley because it has evolved as a unit by a series of interlocking competitive processes and has a definite organization (structure and function). The constituent organisms are adapted to their surroundings, including the adjacent biota, and hence are to some extent dependent on other parts of the community.

Clements, Allee et al., and Tansley regarded communities as organisms or as analogous to organisms because of the seeming unity and interdependence of biotic units in nature. These views did not go unchallenged.

COMMUNITIES AS ASPECTS OF CONTINUA

I have referred briefly to the idea that communities are not objective, clearly defined ecological units, but might be abstractions from continua of distribution. If the organisms of "communities" are randomly distributed, obviously no kind of community superindividual can exist. An early explicit statement of this view is that of Gleason (1926): "Are we not justified in coming to the general conclusion, far removed from the prevailing opinion, that an association is not an organism, scarcely even a vegetational unit, but merely a *coincidence*?" Gleason was particularly impressed by the differences between samples from the same area (no two quadrats are ever exactly similar) and by the chance events in previously uncolonized areas that lead to different results from similar beginnings. The plants growing in an area result from a fluctuating and unpredictable seed-dispersal from near and far, modulated by short- and long-term fluctuations in climate, allowing some marginal species to survive at one time and others at another time: "...the vegetation of an area is merely the resultant of two factors, the fluctuating and fortuitious immigration of plants and an equally fluctuating environment." Because

there is never time for complete spread of seeds between one climatic fluctuation and the next, plant groupings are intrinsically heterogeneous: "Heterogeneity in the structure of an association may be explained by the accidents of seed dispersal and by the lack of time for complete establishment"... "A plant association therefore...represents the result of an environmental sorting of a population." The plants found in one area will grade into the groupings in another area without sharp boundaries unless there is a marked climatic boundary or a marked change in the immigration of species.

Gleason's ideas have been regarded as extreme, but they have polarized views against misty holistic concepts of organismal or integrated communities, and have led to studies of the distribution of plants along environmental or more abstract gradients (for examples and reviews see Whittaker (1956, 1965, 1967)). These studies involve *ordination*, as opposed to the older, hierarchical *classification* of vegetation. Ordination may be *direct*, involving the analysis of patterns along various environmental gradients, or it may be *indirect*, involving "similarity measurements" comparing the abundance or distribution of species or species groups, the construction of plexuses relating samples in terms of ecological distances or computed "similarity values," or the correlation of species by factor analysis (Whittaker, 1967).

Most studies of direct ordination show that species are distributed along environmental gradients in more or less binomial curves of abundance, and the distribution of each species is relatively independent of those of others. This makes anything but arbitrary delimitation of communities very difficult. Despite this, "community" has been retained as a convenient descriptive term, embodying the idea of a complex of intergrading populations. As Whittaker (1967) has stated, there is a "....replacement of the conception of vegetation as consisting of the units into which ecologists have classified that vegetation, units often of unclear relation to one another, by the conception of vegetation as a pattern of intergrading communities, a complex population continuum."

THE COMMUNITY CONCEPT IN MARINE ZOOLOGY AND OTHER DISCIPLINES

The basic similarities between studies of plant communities and those of benthic animals are great. Zoologists, like their botanical confreres, have been concerned with communities as abstract versus concrete units, have regarded quantitative methods as unimportant or important in distinguishing communities, have stressed the importance of overall structure independent of species composition or conversely the importance of dominance, have emphasized classification of community units, have stressed succession and the organismic nature of communities resulting from interlocking competitions and selection, and have even regarded benthic communities as being more or less continua. Their diversity of approaches, the regional differences in views, and the variety of ecological phenomena they have studied have been discussed by Whittaker (1962). Many of the ideas and terms used by marine ecologists seem to have been freely borrowed from plant ecology, with little

careful specification of what is implied and with even less attempt to rigorously verify or disprove the biological principles suggested.

The history of concepts of benthic animal communities is often traced back to Karl Möbius, who late in the 19th century, working at Kiel, put forward the idea of the *biocoenosis* (Hedgpeth, 1957a, b) for oyster beds. It is easy to read too much into Möbius' term, which seems to have referred simply to localized groupings of animals reaching equilibrium with the environment. Although later workers saw in his concept the idea of community homeostasis, this was apparently not directly stated by Möbius.

In a survey of the shallow water animals of the Skagerrak and Baltic Sea, Petersen (1918) found a regular recurrence of a few common species over wide areas, and named eight communities, characterized by one or two most abundant species. According to Thorson (1957), Petersen recognized communities as "statistical" units only, that is, as based on the recurrence of a few large and conspicuous animals, and made no statements about community function. This is largely borne out by Petersen's paper of 1918 in which the role of sediment and other environmental factors in governing distribution is discussed, whereas the only hint of the role of biological interactions is a brief mention of the influence of brittlestar predation on the spatfall of molluscs. There is little indication of the effect of the thinking of northern European plant ecologists in Petersen's summary (1918) of his benthic investigations except for a brief mention of terrestrial vegetation in a footnote and the use of dominants to characterize communities. This may have been derived from Warming, as Hedgpeth (1957b) suggests.

These early ideas, largely descriptive, have been elaborated by later workers, often with the addition of theoretical overtones not present in the original formulations by Möbius and Petersen. The most imposing structure is certainly one originating in America — that presented by Clements and Shelford (1939). Using the groundwork in plant ecology laid by Clements, they list many terrestrial and marine biomes or communities (defined as plant plus animal formations) for North America, in an attempt to unify information about faunas and floras in a single theoretical framework. The system is strongly synthetic and is based on large, conspicuous plants and animals across large geographic areas. It assumes the concreteness and organismic unity of communities, developing through successions. The classification of marine communities, listing 10 biomes for Puget Sound and North Atlantic areas, requires intermediate groupings ("faciations," governed by "subclimates") to maintain coherence. After the passage of 20 years, this attempt at classification now appears an almost meaningless oversimplification. Incomplete faunal and floral lists were forced into a theoretical framework of succession, climax, and organismic unity, ideas which are not supported by any kind of evidence.

Another related classification of benthic communities has been outlined by Jones (1950): communities are separable ecological units, not just artifacts of sampling technique; community structure is primarily imposed by salinity,

temperature, and sediment, and secondarily by light, exposure, oxygen supply, and biological interactions, not by "purely biological factors." Jones' classification of communities is on the basis of zoogeographical distribution, depth, and sediment. This scheme avoids using faunistic evidence, and thus avoids the problem of overlapping distributions. It also avoids, of course, the important problem, basic to community ecology, whether the biological features of the communities (such as the abundance and diversity of species and their competitive interactions) are meaningful in the establishment and maintenance of the groupings seen in nature.

Thorson (1957, 1958) has presented one of the most widely used and discussed concepts in marine ecology, that of *parallel communities*. Similar ideas have appeared before, for example in Edward Forbes' "law of representation" (Thomson, 1873, p. 8) which stated that under similar environmental conditions, similar species are found everywhere in the world. Thorson presents his idea with particular impact and clarity, using as a basis Petersen communities with markedly dominant species. Although communities are in a broad way governed by environment, they are functionally integrated, according to Thorson, the evidence and results being as follows:

(1) Pelagic larvae of invertebrates do not just settle passively, or at random, but actually choose favorable substrata and may delay settling if a favorable environment is not encountered immediately.

(2) Larvae, through predation, are exposed to intense selection pressures.

(3) Because of intense predation pressure, benthic organisms often produce larvae during "passive periods" of predators (for example during the breeding periods of brittlestars). This results in selective advantage to both prey and predators, since the larval mortality of prey species is reduced and predators obtain a larger, more energy-rich meal by utilizing the prey later in life. Members of the community are thus bound together by their adaptations to each other.

(4) The same types of communities are found in similar environments all over the world. These parallel communities reflect similar ecological responses by groups of more or less closely related species in different geographical areas.

The implications of Thorson's ideas are that because of similar selective forces and responses to them we can expect to find closely similar animals under similar environmental conditions no matter where we look. Environments, interacting with the adaptations of closely related and functionally similar species, give rise to real, definable parallel benthic communities which are, within themselves, integrated and coadapted. Benthic communities, in this view, are not just abstractions from species lists, but concrete, biologically organized, ecological entities, and are a complex function of adaptations to particular environments.

This concept, if adequately supported by studies demonstrating the coherence of communities, is of major importance. But Thorson (1966) has been forced to qualify his views. In some tropical areas benthic groupings have been discovered which defy classification into parallel communities, since they are incredibly diverse, with few abundant species and a preponderance of rarer ones. Although little published evidence bears on this yet,

it seems very likely that vast areas characterized by stable environments, such as the tropics and the deep-sea (Hessler and Sanders, 1967; Sanders, 1968) have highly diverse "communities" that resist objective classification by numerically abundant or metabolically important species, and which grade into adjacent assemblages. A closer look at parallel communities in temperate zones with emphasis on the rarer species and with adequate sampling along gradients, will probably give similar results even when abundant or conspicuous species are present. Some work now in progress supports this contention. Figure 1 shows the densities of benthic animals along a transect from low water

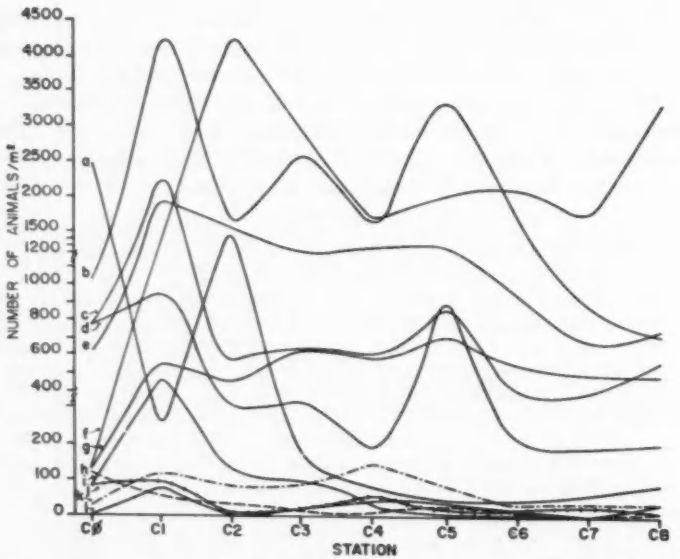

FIG. 1. The abundance of benthic animals at five stations along a transect of an intertidal sand flat at Lawrencetown, Halifax Co., Nova Scotia, in July 1968. (*a*) Oligochaete species B; (*b*) *Hydrobia* sp; (*c*) *Macoma balthica*; (*d*) *Mya arenaria*; (*e*) oligochaete species A; (*f*) *Pygospio elegans*; (*g*) *Chiridotea caeca*; (*h*) *Scolecolepides viridis*; (*i*) oligochaete species C; (*j*) *Heteromastus filiformis*; (*k*) *Eteone longa*; (*l*) *Polydora ligni*.

to high water level on a sand flat near Halifax, Nova Scotia. Although four abundant species peak together at one station (C1), as one might expect if a discrete community were present, some of the curves of abundance are out of phase at other stations. Several smaller and less abundant infaunal species show no obvious correlation with the peaks of abundant species and appear to have independent distributions. It is thus just as legitimate to regard the community as an abstraction from a series of continua as to characterize it in terms of a few abundant species.

The problems of the nature of benthic animal communities bear careful scrutiny, partly because of the basic importance of learning what the ecological units are really like, and partly because ideas from benthic ecology are finding increasing use by paleoecologists (Hedgpeth, 1957a, b; Johnson, 1964), who are interested in the evolution of communities and the interpretation of fossil assemblages as remnants of biotic assemblages. The paleoecologists' problems in interpreting the history of fossil assemblages and an admirable account of viewpoints in marine benthic ecology have been presented by Johnson (1964), who takes a pragmatic view of a community as "the assemblage of organisms inhabiting a specified space," and defines *community type* as "an assemblage of organisms which often occur together." This kind of approach is not typological, but pragmatic, as will be discussed in another section.

Enough evidence has accumulated to show that the word *community* is used in several ways. Even in a single study communities may be regarded as highly integrated and definable entities or as abstractions from unintegrated continua of distribution (for a good example and discussion from terrestrial ecology, showing that this is not unique to marine zoology, see Brewer (1967)). To date, no firm, unequivocal evidence allows us to decide which view is most meaningful or if these alternatives are the only ones.

SPECIES CONSTANCY AND DYNAMIC STABILITY

Macfadyen (1963) briefly reviews the various uses of the word *community* by ecologists. As he states, the abundant ecological work on communities indicates that communities, if integrated units, should show "the properties of species constancy, dynamic stability and organismic unity."

The importance of stability has been stressed in many discussions of ecological communities, in particular those that use the concept of ecological climax. MacArthur (1955) has shown, using an approach from information theory, that increasing the number of alternative pathways for energy flow through a community (by increasing the number of trophic levels and therefore the number of species involved, or by increasing the number of species available to a predator without increasing the number of trophic levels) will increase its stability. Leigh (1965), using the Volterra equations reaches the same conclusions. Stability of numbers may also result from genetic adaptation (by "genetic feedback") between prey and predator, as Pimentel has shown in a series of laboratory experiments (for summary, see Pimentel, 1968); this is the sort of situation one would expect to find in highly integrated communities where species have evolved together in an environment of selective forces, both physical and biotic.

There are some clues from the literature that species constancy and dynamic stability may not be characteristic of some marine communities. For example, under the heading of the "Syndosmya Community," Thorson (1957) says "The standing crop will comprise the production of little more than a year, or perhaps a fraction of it, and the total productivity is very large.

Fluctuations of the quantitative composition of the community from year to year are enormous. A species dominating one year may be absent or nearly absent and replaced by another species the next year." In describing the "Boreo-Arctic Ampelisca Community," Thorson (1957) states "Characteristic animals: large numbers of different species belonging to the amphipod genus *Ampelisca* ... The character and distribution of this community is not at all clear. It seems to occur in patches in other communities...".

There is further evidence on the nature of instability in an *Ampelisca* community which shows its importance in a complex assemblage of marine animals. In the summer of 1960, the amphipod crustacean *Ampelisca abdita* (for an account of its biology see Mills (1967)) appeared on an intertidal sand flat in Barnstable Harbor, Massachusetts. The flat had previously been dominated in the summer by the gastropod *Nassarius obsoletus*, which occurred in vast aggregations over large areas before moving into the deeper water of the subtidal channels in the fall. This flat was surveyed by Sanders et al. (1962) in the summer of 1959. Compared with other flats in Barnstable Harbor, the *Nassarius* flat (station E) had an unusually low number of individuals, low biomass, and low chlorophyll concentration (Table 1). The effect of *Nassarius* on the infauna is great. Large numbers of the snails sharply reduced

TABLE 1. Some features of the *Ampelisca* flat at Barnstable Harbor, Massachusetts (data for 1959 from Sanders et al. (1962)).

Year	No. species	No. individuals	Median grain size of sediment (*mm*)	Silt–clay (%)	Chlorophyll *a* (mg/m^2)
1959	36	6,711	0.14	5.54	217
1962	25	80,450	0.074	6.91	1. Tubeless sandy areas: 354.7±97.5 (SD) 2. Tube areas, incl. tubes: 798.5±155.1 (SD)

the numbers of infaunal animals, apparently by disturbing the sediment mechanically; and the reduction of chlorophyll *a*, probably due to the grazing of the snails, may also have played a role in reducing the infauna (Grant, MS, 1965). A breeding group of *Ampelisca* probably encountered the flat in the fall of 1960 or spring of 1961 and were able to colonize it because of the low density of infaunal animals present.

The biology of *Ampelisca abdita* on the flat has been discussed in detail elsewhere (Mills, 1967). An overwintering generation produces young in the spring when the water temperature reaches approximately 10 C. The ensuing summer generation grows rapidly and produces young from late June to early fall; its offspring are the next overwintering generation. Even in winter, densities on the flat were very great, and the areas colonized were always

thick with close-packed tubes which often covered areas hundreds of square meters in extent. The appearance of such dense aggregations was accompanied by marked changes in the fauna (see Mills, 1967, table XI). By the summer of 1960, when *A. abdita* began to appear on the flat, the number of species increased to 42, and many of the species present in 1959 had increased greatly in abundance. In January 1962 a number of species had disappeared, perhaps a seasonal effect not due directly to the presence of *Ampelisca*, but the number of individuals was very high, exceeding previous densities even when *Ampelisca* is excluded from the total. Many of the faunal changes must be associated with the presence of *Ampelisca* tubes. The flattened, parchmentlike tubes increased the available surface area of the flat three to five times, giving more surface area for the growth of flagellates and benthic diatoms (shown in increased amounts of chlorophyll *a*, see Table 1), and vastly increasing the topographic complexity of the area. The last feature accounts for the increased abundance of many of the small infaunal polychaete worms, which, being selective deposit feeders, were favored in the food-rich areas between *Ampelisca* tubes.

As well as changing the biological environment, *A. abdita* modified its own physical environment. This species is largely a selective deposit feeder which puts fine organic material and sand grains into suspension by the rotary beating action of the second antennae (Enequist, 1960; Mills, 1967). Some degree of filter-feeding may also occur as tidal currents carry suspended material across the flat. Large particles are rejected, and the material ingested is composed of amorphous organic material, diatoms, probably flagellates and bacteria, and very fine sand grains. Fecal rods are extruded about the tubes, consolidating the fine material ingested. The effect of feeding is to increase the proportion of fine particles about the tubes. This is shown in a decrease in the median grain size of the sediment between 1959 (when *Nassarius* was present) and 1962 (Table 1). The soft, spongy nature of the *Ampelisca* areas was obvious in going from them to other areas of the flat. The sand flats in this part of Barnstable Harbor are quite stable in form and appear to be in dynamic equilibrium with tidal currents. The decrease of median grain size associated with aggregations of *Ampelisca* was bound to cause instability, that is, susceptibility to washing out. Relatively minor breaks in the mat of *Ampelisca* tubes were sufficient to cause large areas to wash out, especially on windy days when the tide was rising or falling over the flats.

At breeding times (early May, and late June–August), many *Ampelisca* leave their tubes and swim for a time in the plankton. The peaks of swimming activity appear to be correlated with high tide and full moon (Mills, 1967). Adult males, in particular, are well-adapted for swimming since at their terminal molt the body becomes highly streamlined and the antennae are lengthened and become well-provided with sensillae, presumably for finding females. Females with eggs apparently leave the plankton and settle in previously uncolonized areas. During the summer breeding periods I observed dense aggregations of the tiny tubes of newly released juveniles in areas not previously

colonized. The exodus has two major effects. It ensures that the juveniles occur where they will not face intense competition from the remaining adults, and it places them in areas of the flat which are physically stable and not liable to wash out. It also results in the abandonment of old areas of colonization and their occupation by other species.

The biology of *Ampelisca abdita*, particularly its modification of the sediment and its forays into the plankton when the females are carrying eggs and young, helps to account for its appearance and disappearance in Barnstable Harbor, and for Thorson's (1957) observations of the high productivity, short generation time, and change in species composition of the "Syndosmya Community" (which in some areas contains species of *Ampelisca*) and the "Boreo-Arctic *Ampelisca* Community." Species of *Ampelisca* appear to be adapted in their quick growth to crowded conditions (Mills, 1967), and in their reproductive migrations to the modification of environment which results from their feeding activities. They are in a sense "fugitive species," (Hutchinson, 1951, 1965; Slobodkin, 1961); that is, being adapted to frequent changes of the area occupied, they probably seldom have an opportunity to come to competitive or symbiotic equilibrium with other species in the community or to be eliminated by them. Their dramatic changes in numbers result in changes of the associated species. Species constancy, then, is unlikely to hold for communities dominated by *Ampelisca* spp. and these communities, rather than showing "dynamic stability," show a dynamic instability resulting from the modification of sediment and the need to move from areas of physical instability.

DEFINING COMMUNITIES

It is clear from the historical and ecological discussions that a variety of complex ecological assemblages exist. These range from loosely integrated aggregations (or even simple co-occurrences of species independently distributed along continua) to highly stable coadapted groups in equilibrium with climate and other environmental factors for long periods of time. Groups, previously unexamined, in which instability may be biologically produced rather than imposed directly by changes in the physical environment also exist. Perhaps it is asking too much of a single word, "community," to cover such a range, but the alternative is a series of terms, each arbitrary, setting boundaries where no clear ones exist. The disadvantages of coining new terms can be seen by examining any dictionary of ecology, so it seems best to retain the word "community," recognizing that its meaning will vary from use to use and with users, not necessarily consciously. It may at times denote a hypothesis, or at others may be simply a list of co-occurring species, depending on the user and the rigour of his usage.

In concluding his discussion of ecological communities, Macfadyen (1963) takes the moderate and practical view that ecological communities are a "working hypothesis." With this in mind, because a variety of ecological

phenomena are encompassed by the term, I suggest that biotic communities must not be rigorously defined (as abstract units of a classification may be, for example), and that the word *community* must have a practical meaning. By combining definitions offered by Hedgpeth (1957b) and Macfadyen (1963), *community* means *a group of organisms occurring in a particular environment, presumably interacting with each other and with the environment, and separable by means of ecological survey from other groups.*

This definition is consistent with modern usage (Johnson, 1964; Fager, 1963) and with many earlier definitions (e.g., Clements, 1916; Tansley, 1920; Allee et al., 1949; Thorson, 1957) but is less conceptually loaded than the early approaches, leaving the ecologist free to investigate biological relationships (and eventually to express them in a quantitative way) without unwarranted presuppositions.

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Distinctive Aspects of the Ecology of Stream Fishes: A Review[1]

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The essential feature of a stream is the continuous flow of water, and the various schemes of classification of streams and the associated fish fauna are largely based on factors which determine the average velocity. These schemes have been better developed in Europe than elsewhere, probably due to the relative uniformity of the climate. The characteristic features of fish inhabiting the more rapid streams can be related to the constraints imposed by this environment, and particularly by the need for the population to maintain its position against the continuous tendency of the stream to transport it downstream. Physiological factors associated with the normally high oxygen level and the need for continuous activity include a high routine metabolic rate, a high oxygen threshold for full activity, and, possibly, a high lower lethal limit for dissolved oxygen. Adult fish maintain their position either by continuous swimming in midwater, and these usually have a streamlined shape which is circular or laterally compressed in cross-section, or by avoiding the current and living closely attached to or in the substrate and these are usually dorso-ventrally depressed. The eggs are usually protected from the current by burying them in the substrate, sometimes in a well-developed nest. The general absence of vegetation in rapid streams results in the fish generally feeding principally on the available animal food, usually small invertebrates taken either in the drift or off the bottom. The solitary territorial behaviour which characterizes most stream-living fish probably leads to more even distribution and more efficient utilization of the food supply.

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IN REVIEWING the ecological characteristics of stream-living fishes it is first necessary to consider what are the essential features of a stream, and to examine the requirements which these features impose upon fish inhabiting the streams.

CLASSIFICATION OF THE ENVIRONMENT

Essentially, streams are bodies of water flowing more or less consistently along fairly defined courses. They vary greatly in their size, velocity, gradient, nature of bed, and other features. At one extreme there is the steep mountain torrent, or indeed the waterfall, and at the other the muddy, weedy stream of very slow flow which may grade imperceptibly into the pond or lake. Each major stage in the series between these two extremes can be regarded as having a particular set of environmental features and, in a given geographical region, will be characterized by a particular assemblage of fish species. In general, as streams proceed from source to mouth they tend to pass progressively

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through the stages from the steep torrent to the sluggish, meandering waterway, although there are of course many local exceptions.

There have been a number of attempts to define particular stages in these series and to associate them with particular fish faunas. Generally, these schemes of classification have only been applicable to local conditions, and they seem to have been more widely accepted and used in Europe than elsewhere. This European success in the classification of stream types may be due, at least in part, to the relatively narrow climatic range and small number of fish species involved compared, for example, to conditions in North America. Some workers have divided the whole course of a stream or river into only two or three types (Carpenter, 1928), but a widely used scheme is one involving four categories which has been intensively examined by Huet (1959). The four zones in this scheme have been named from the characteristic fish species found in them. In descending order of average current, and therefore of location on most streams, they are:

(1) The trout (*Salmo trutta*) zone;
(2) The grayling (*Thymallus thymallus*) zone;
(3) The barbel (*Barbus barbus*) zone;
(4) The bream (*Abramis brama*) zone.

Huet has pointed out that each of these zones is characterized by a particular set of combinations of stream gradient and stream width, and has expressed these in a single diagram (Fig. 1). Since, for a given gradient, the average velocity of a stream tends to increase with the area of cross-section (or the width), the effect of the boundaries given to each zone in the diagram is to make the average velocity in each zone more or less independent of the size of stream. Most streams tend to consist of an alternation of rapids or riffles and of pools, and diminishing gradient is normally accompanied by a diminishing proportion of rapids in the stream course and by an increase in the proportion and often in the size of pools. The two extremes are, of course, streams consisting entirely of rapids, and streams of quiet even flow which are, essentially, continuous pools. There is, also, a close relation between the velocity of a stream and the size of the particles in its bed; diminishing velocity is generally accompanied by diminishing particle size.

In North America the climatic range is much wider than in Europe, partly as a result of the greater ranges in both latitude and altitude. The freshwater fauna also consists of a larger number of species and represents more taxonomic groups. It is probably as a result of these features that less success has been achieved on this continent than in Europe in identifying characteristic stream environmental types and associating them with particular communities of fish species. Perhaps the only comprehensive scheme which has been proposed for North American streams is that of Lagler et al. (1962) who proposed a scheme dividing streams into five zones on the basis of their physical characteristics. Although they did not define the physical characteristics of their zones in detail comparable with that of Huet, they listed characteristic fish species as assemblages for each zone. In order of descending gradient or velocity these were:

(1) grayling
(2) stream char
(3) flowing water minnows and pike
(4) basses
(5) catfishes, suckers, and quiet water minnows.

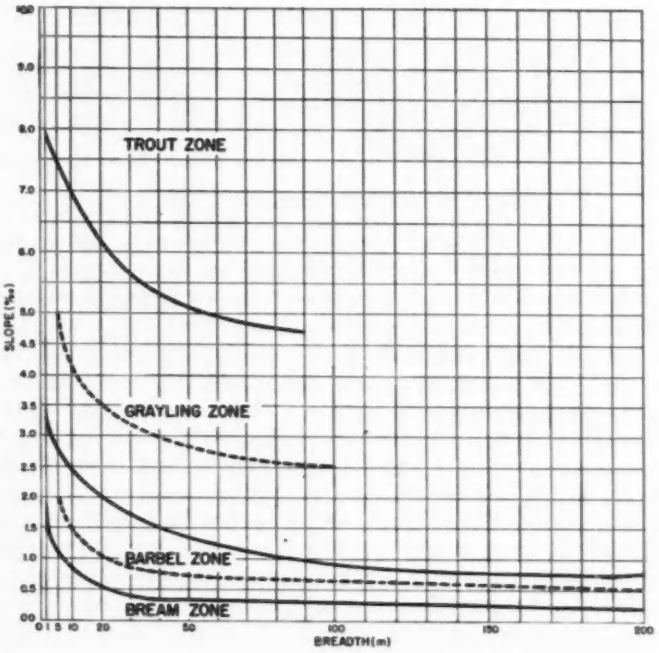

FIG. 1. Influence of gradient and width on the characteristic fish fauna of European streams (from Huet, 1959).

It is unfortunate that in selecting the species designated as characteristic of the various stream types in this scheme, effects due to climate and broad geographical distribution have apparently been confused with those due to the essential stream characteristics derived from gradient and velocity. The species named as representative of the first two stream types, grayling and stream char, are essentially northern in their distribution whereas the basses are essentially southern. There is, in fact, only a very limited degree of overlap between the distribution of the first two groups and that of the basses and the separation between them appears to be due more to climatic and dispersal effects than to stream gradient or velocity. On the other hand, such groups as the basses and the catfishes include species having fairly different environmental requirements. The broad groupings used in this scheme therefore lead to overlaps which could be avoided by a more restricted definition of

characteristic species. The channel catfish, for example, although a representative of group (5), is normally found in much more rapid water than the largemouth bass, a representative of group (4).

When applied within very limited areas, so that broad climatic and distributional effects are avoided, vertical zonations of fish species such as those described in different parts of the middle west by Shelford and Eddy (1929) and Thompson and Hunt (1930) probably reflect the results of zonation in gradient velocity.

Outside the north temperate region little data seem to exist regarding the ecology of stream fishes and the effects of environmental factors upon their distribution, and no classifications of stream types and associated fish faunas seem to have been proposed.

DEMANDS OF RAPID STREAMS

The remainder of this review will be concerned with the ecology of fish inhabiting streams in which the dominant current is at least fairly rapid, so that its influence and that of the associated environmental features is clearly developed. Such streams would correspond approximately to the trout and grayling zones of Huet, and, possibly, to the grayling and stream char zones of Lagler et al. These streams normally contain a relatively high proportion of rapids or riffles, and the pools, although they may be frequent, tend to be small in area. Their beds are usually composed predominantly of rocks, boulders, and coarse gravels, and they support little rooted vegetation. The algal flora is commonly limited to a thin film over the stones, although under some conditions it may form thick mats. Dissolved oxygen tends to be at a high level at all times of the day and night. This is primarily due to the excellent interchange between air and water which the turbulent flow provides, combined with a fairly low rate of utilization of oxygen by plant respiration in the hours of darkness. It is also commonly believed that at least in temperate climates such streams tend to have relatively low temperatures. Where this does occur it is probably the result of a combination of higher altitude, shorter length of course over which warming can take place, and the more effective shading by trees which can occur on relatively narrow head-water streams. A great many exceptions could, however, be found to this generalization.

The fish which live in these waters must be adapted in their structure, requirements, and way of life to the particular conditions there. The essential feature of this environment is the continuous downstream movement of the water, and fish which live in it must therefore be able, over their life history as a whole, to resist this movement and thus maintain a localized population. They must also be able to obtain their food from the resources available in an environment consisting of flowing water and a stony substrate. Compensating to some extent for these demands imposed by the environment is the absence of any need to tolerate low oxygen conditions or, commonly, high temperatures. Ability to withstand low temperatures and some degree of ice formation may, however, be an essential characteristic in some locations.

METABOLIC EFFECTS

It is frequently stated that, as a general rule, fish living in rapid streams have a higher oxygen requirement than those living in still or more sluggish waters. Wunder (1936) for instance, arranged a number of species of European freshwater fish in four groups closely corresponding to those characterizing Huet's four zones and described these groups as (1) fish species with a very high oxygen requirement; (2) fish species with a high oxygen requirement; (3) fish species with a medium oxygen requirement; and (4) fish species with a slight oxygen requirement. He provided, however, little data to support this grouping. More recent studies have shown that simple measurement of oxygen tolerance, and particularly of the lower lethal limit, may have little ecological significance. It is much more important to consider the requirements of the fish at the levels of activity which successful life in their natural habitat requires. One index of this is provided by the minimum oxygen concentration at which the fish can be fully active as measured by its ability to maintain its full swimming speed. In most fish the maximum sustained swimming speed remains fairly constant as oxygen concentration is reduced below saturation until a critical value is reached, and below this the maximum sustained speed falls off rapidly with further reduction in oxygen. Data are available on this critical level for full activity for a few species of freshwater fish occupying different habitats. For brook trout (*Salvelinus fontinalis*) and yearling coho salmon (*Oncorhynchus kisutch*) which both live in the more rapid stream environments corresponding to zones (1) and (2), the critical oxygen levels appear to be about 6 ppm (Graham, 1949), and 7–8 ppm (Davis et al., 1963) respectively. For the European perch (*Perca fluviatilis*) which typically inhabits still waters and the quiet streams of Huet's zone (3) the data of Ferguson quoted by Fry (1957) indicate a value of about 3 ppm. For the largemouth bass, an inhabitant of still or very quiet waters, Doudoroff and Warren (1965) report that swimming speed is independent of oxygen concentration down to 5 ppm but their data indicate that even down to 2 ppm the rate of decline in activity with diminishing oxygen is much less than for any of the other species quoted.

In a more direct approach to the problem, Clausen (1936) measured the routine metabolic rate, as determined by rate of oxygen consumption, for a number of Illinois stream fishes. He found that, when arranged in order of diminishing metabolic rate, the fish examined came in the following order:

(1) Greenside darter (*Etheostoma blennioides* Raf.)
(2) Stoneroller (*Campostoma anomalum* (Raf.))
(3) Creek chubsucker (*Erimyzon oblongus* (Mitchill))
(4) Common shiner (*Notropis cornutus* (Mitchill))
(5) Golden shiner (*Notemigonus crysoleucas* (Mitchill))
(6) White crappie (*Pomoxis annularis* Raf.)
(7) Black bullhead (*Ictalurus melas* (Raf.))
(8) Largemouth bass (*Micropterus salmoides* (Lacépède)).

From a comparison of these results with data on the distribution of these fishes published by other workers, Clausen concluded that this order of metabolic rates corresponded almost exactly with a diminishing order of velocity in the waters which the fish normally inhabited. The first three species would probably be characteristic of Huet's or Lagler's two most rapid zones, whereas the last three or four would be found normally in the two most quiet zones. Thus Clausen's results suggest that fish living in fairly rapid streams tend to have higher routine metabolic rates than fish living in quieter waters.

Probably the best summary of the relation between habitat and metabolic rate in fishes is that of Winberg (1960) who states: "Perhaps it can be regarded as established, or at least very likely, that typical limnophilic fish have a routine metabolic rate lower than average, whereas typical rheophiles have a higher one. However, it is hard to say how widely this rule can be applied, how large a circle of species it embraces, or to what extent the level of metabolism differs in extreme and typical cases; and furthermore, what are the relative roles of individual acclimation and species adaptation. It seems to me that the level of metabolism of rheophilic fish could scarcely be more than 1.5–2 times that of limnophilic fish.

"From the fact that levels of routine metabolism of species which differ ecologically are often similar or even identical, we should by no means conclude that under natural conditions there are no ecologically-determined differences in the metabolism of different fish. On the contrary we have every reason to believe that they can be strongly developed, but not in respect to resting metabolism, which mainly determines the magnitude of the routine metabolism — instead, in respect to active metabolism. Ecological differences concern first and foremost the moving, active fish; they determine his mode of life and degree of activity. To a much larger extent than can the resting metabolism, the active metabolism reflects the multiformity and specificity of different kinds of adaptation — to prolonged or brief periods of movement, to movement at a constant or at a changing speed, at different efficiences, and so on."

SWIMMING BEHAVIOUR

If an adult stream-living fish is to be able to maintain its position, and this is essential if the species is to continue to occupy the area, it must have the ability to withstand the downstream force of the current. This it can do by a combination of swimming against the current and resting in positions where it either avoids the current's effect, or obtains mechanical support against it. Maintenance of position against the current by swimming implies a positive rheotactic response and this has been demonstrated to have a visual basis in many fish. Although most stream-living fish make use of both upstream swimming and avoidance to maintain their position, the fish inhabiting fairly rapid waters tend to fall into two categories. In the first category are those which spend most of their time in midwater or close to the surface; generally these are swimming steadily against some degree of current for much of the

time, although most species often occupy sheltered positions where the velocity is reduced. These fish tend to be well-streamlined forms, circular or slightly laterally compressed in cross-section, and are generally regarded as active or powerful swimmers. Typical examples of this group are the trouts and salmons, the graylings, and some of the stream-living minnows. The other category consists of fish which normally live on the bottom, either pressed tightly to exposed surfaces or in the crevices between rocks and stones. Many members of this group can swim rapidly over short distances and customarily change their position in this way. Others, and this includes some forms living in very rapid waters, can only swim feebly and move about by wriggling through the fissures in the bottom. The fish in this group are generally strongly depressed vertically and often have a flattened ventral surface. The pectoral and sometimes the pelvic fins are enlarged and often modified to provide increased adhesion to the bottom and the dorsal fins are often large and strong. The group includes fish from a number of distinct and unrelated families, although they all have a strong superficial similarity. Among them are the darters (Etheostomatinae), the sculpins (Cottidae), and the freshwater gobies (Eleotridae).

REPRODUCTION

Although the stream fish which live above the bottom are commonly regarded as strong swimmers there appear to be few data to support this belief. The only directly relevant study that I have found is that of Bainbridge (1960) who measured the speeds sustainable for periods from a burst of minimum duration up to 20 sec for rainbow trout (*Salmo gairdneri*), for the European dace (*Leuciscus leuciscus*), a fish typical of Huet's barbel zone, and for goldfish (*Carassius auratus*). Rather surprisingly he found that the rainbow trout was inferior to the other two species for all durations except the minimum burst. Bainbridge (1962), however, recognized the possibility that his trout, which were of a stock which had been cultured for many generations, could have been inferior in performance to wild fish.

In addition to requiring that the adult fish should be able to maintain their position, the stream environment also imposes special demands on the eggs. The first need is that they should be able to remain within the stream system, and, generally, in the same locality, throughout the period between deposition and hatching. This implies that they must be able to resist, or be protected from, the downstream action of the current. Wherever they are placed they must also be able to obtain sufficient oxygen, and, therefore, if they are placed in sheltered situations these must provide an adequate circulation of water and excessive silting must be avoided. The eggs must also be so placed that they are protected from mechanical damage either from objects moving in the current or through being dislodged and swept downstream in floods. The need to meet these requirements greatly influences the spawning habits of stream fish. It is not surprising to find that fish living in this environment rarely scatter their eggs at random or even attach them to the exposed

surfaces of fixed objects. Many of them, such as the Salmonidae and stoneroller minnows, have well-organized nest-building behaviour which leads to their eggs being buried some distance below the surface of a stony stream bed. Others, including most of the darters, sculpins, and gobies, attach their eggs to the undersurface of large stones and other objects in the stream bed. Some of these fish show some nest-building behaviour in that they excavate the cavities in which the eggs are laid and subsequently buried, but other species simply take advantage of natural cavities for this purpose. The European grayling does not appear to form nests but the spawning female forces the caudal part of the body well down among the stones of the bottom by strong vibrations and digging movements so that the eggs are inserted directly in the crevices among the stones (Fabricius and Gustafson, 1955). Somewhat varied forms of spawning behaviour are found in the stream-living minnows. Most of them build definite nests or otherwise bury their eggs, but in a few, such as the blacknose dace (*Rhinichthys atratulus*), the eggs are scattered and drift into crevices in the bottom where they adhere (Traver, quoted by Hubbs and Cooper, 1936). The general spawning characteristics of stream fishes are strikingly illustrated by the classification of spawning behaviour drawn up by Lagler et al. (1962). In this, nearly all the examples quoted for nest-building behaviour in the widest sense, and very few of those for other kinds of spawning behaviour, are provided by stream-living fish.

FEEDING HABITS

The food of stream-living fishes is of course limited by what is available to them. Since in most streams of the kind under discussion little vegetation occurs, the fish inhabiting them must generally make use of animal food. In the great majority of cases the principal component is the invertebrates and particularly the insects of the bottom fauna, although some salmonids, for example, will prey on the smaller fish, particularly when they are large. The two principal methods of feeding appear to be to pick up the insects individually from the bottom, and to intercept them as they drift down with the current. The bottom-living fishes probably feed almost entirely in the former manner but most of the species in the midwater group, such as the salmonids, employ both methods of feeding in varying proportions. In many instances the method will change both seasonally or with the time of day according to the relative availability of food from the two sources, drifting food commonly being most freely taken in the evening and early morning when the largest numbers of animals are coming down with the current (Waters, 1962). Even within this group there are considerable differences between species in the relative extent to which they feed off the bottom and in midwater. Young stages of the coho salmon, for example, take a particularly high proportion of drifting food. All species which feed on drifting organisms obtain much of their food not from the stream itself but from the small terrestrial animals falling onto it.

There are, however, a few stream-living fish which feed regularly on plants and form exceptions to this rule — e.g., the Japanese ayu (*Plecoglossus altivelis*) which feeds on algae atatched to stones on the stream bed (Kawanabe, 1969), and the stoneroller (*Campostoma anomalum*) (E. L. Cooper, personal communication).

SOCIAL BEHAVIOUR

A further characteristic of stream-living fishes is that for most of their lives they are solitary and sometimes strongly territorial, and rarely show schooling behaviour. Territorial behaviour will ensure that the fish are spread rather evenly over the stream bed, and tend to cause the food supply in all physically suitable localities to be utilized to about the same extent by either drift-feeding or bottom-feeding fish. Kawanabe (1969) has, however, shown that the ayu is strongly territorial at low population densities, but that this behaviour breaks down and the fish begin to school when the population density rises above a certain critical level. Under these conditions the food supply on the stream bed is able to support a fish population more dense than the maximum territorial behaviour would allow, so that territoriality in this instance, if it did not break down, would actually restrict the quantity of fish the stream could produce. However, although this is the situation in species which feed principally on the algal vegetation, no similar breakdown of territoriality seems to have been described in a fish which takes animal food and thus utilizes a higher trophic level with a correspondingly lower food production rate.

The change from a territorial and solitary mode of life while feeding in fresh water, to a school existence when the downstream migration commences, is striking in many salmonids (e.g. *Salmo salar*). Some other stream fish only form schools during the spawning season.

CONCLUSION

To sum up, the characteristics commonly found in the fish adapted to life in the fairly rapid streams which constitute the trout and grayling zones in North Temperate regions are: (1) possibly a high lower lethal limit for dissolved oxygen; (2) a high oxygen threshold for full activity; (3) a high routine metabolic rate; (4) either a well-streamlined shape and ability to maintain themselves against a current by active swimming, or a flattened shape associated with the habit of remaining closely pressed to the bottom or in crevices within it; (5) protection of the eggs by burying them in the stream bed either with or without definite nest building; (6) feeding on mainly small invertebrates, especially insects, either by taking them off the bottom or as they drift down with the current, also sometimes feeding on smaller fish; (7) a solitary or territorial mode of life.

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Distributional List of Fishes in the Missouri Drainage of Canada

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WILLOCK, THOMAS A. 1969. Distributional list of fishes in the Missouri drainage of Canada. J. Fish. Res. Bd. Canada 26: 1439–1449.

The presence of possible migration routes between the Missouri (Gulf of Mexico) and adjacent Saskatchewan (Hudson Bay) drainages is briefly discussed in regard to postglacial dispersal of freshwater fishes. A checklist of 9 families and 27 species of fish recorded from the Milk and Frenchman rivers of Alberta and Saskatchewan is provided. Two of these are new to the Missouri ichthyofauna of Canada and definite records of 10 species are reported for the first time from the Missouri drainage of Saskatchewan. Notes are included on the distribution of all known species within the Missouri drainage of Canada. The possible presence of three additional species is discussed.

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INTRODUCTION

THE NORTHERN-MOST TRIBUTARIES of the Missouri River system are the Milk River in southern Alberta and its confluent, the Frenchman River of southwestern Saskatchewan. With at least two possible migration routes existing between these rivers and tributaries of the South Saskatchewan River (Hudson Bay drainage) a few miles to the north, this area is of prime interest to those studying the post-glacial dispersal of middle North American freshwater fishes.

The most westerly of these two connections is the United States St. Mary's Canal which channels water from the St. Mary's River of the South Saskatchewan system into the north fork of the Milk River at the 49th parallel. The second and less direct linkage of the two systems is an intermittent one resulting from an irrigation development in the western portion of the Pakowki Lake interior drainage.

A third possible migration route was formerly provided by a small pond, located on the east slopes of the Cypress Hills. Two streams are reported to have originated from this pond, one joining with South Saskatchewan tributaries, the other with tributaries of the Frenchman River. It has since been destroyed (Stegner, 1955).

The Missouri drainage in Canada and possible migration routes to the South Saskatchewan River are shown in Fig. 1.

This paper presents data on the contemporary distribution of fishes presently found in the Missouri drainage of Canada. A more detailed account, relating the ecology and distribution of Milk River fishes to the area's glacial

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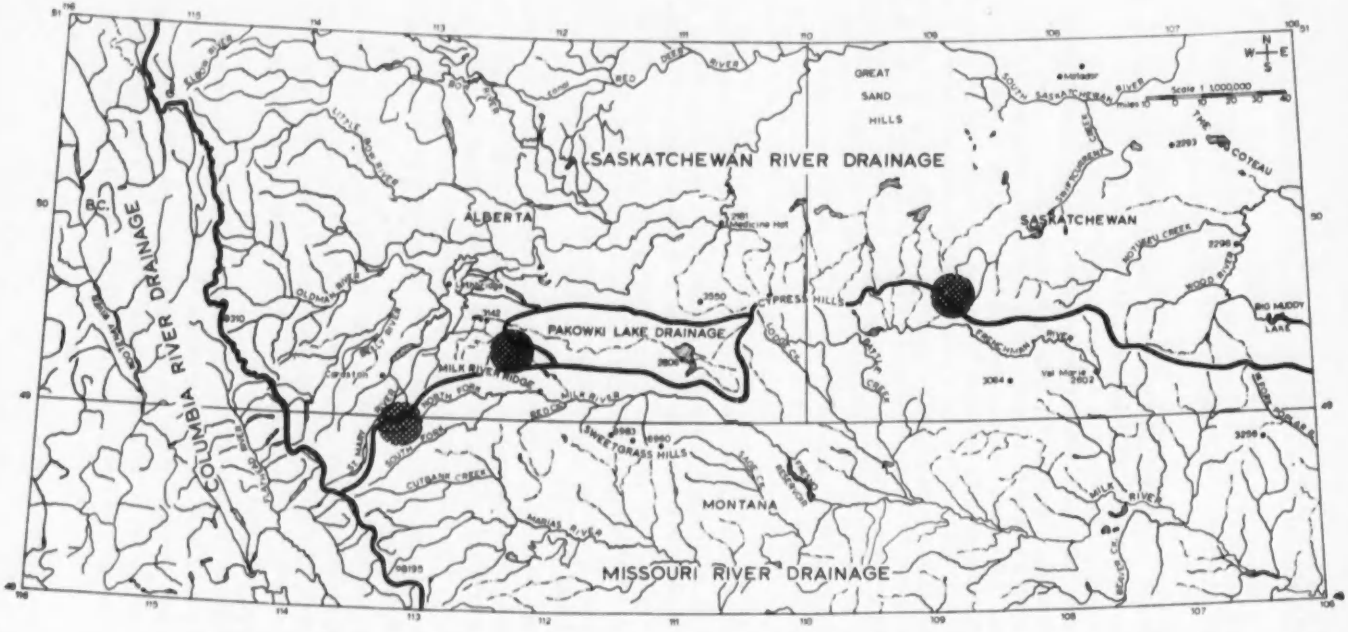

FIG. 1. Region along the Canada–United States boundary containing headwaters of the Pacific, Hudson Bay, and Gulf of Mexico drainages. Heavy solid lines indicate drainage divides and cross-hatched circles show locations of possible migration routes between the Missouri and South Saskatchewan drainages.

history, postglacial dispersal routes, geology, physiography, etc., is being prepared by the author.

In addition to the Milk and Frenchman rivers, the Missouri has three smaller tributaries in Canada. These three, located on and to either side of the 106th meridian, are, from east to west, Big Muddy Creek, Poplar Creek, and Willow Creek. Because of their proximity to tributaries of the Souris River (Hudson Bay drainage) a study of the ichthyofauna of these streams could be valuable.

Unfortunately, the literature on the fishes present in the Milk and Frenchman rivers in Canada is extremely sparse. Chronologically, Atton and Johnson (1955), Scott (1957), Atton (1959), McAllister (1962), Nursall and Lewin (1964), Willock (1968), and Henderson and Peter (1969) have discussed only the occurrence of certain species in the area. Scott and Crossman (MS, 1967) and Willock (1968) have presented incomplete checklists of the ichthyofauna of the Gulf of Mexico watershed in Canada and of the Milk River drainage of Alberta respectively. Except in a brief reference to the occurrence of *Moxostoma aureolum* in "the southwestern portion of the Province," Rawson (1949) does not mention the Frenchman River drainage nor its fauna.

On the other hand, Rawson frequently mentions the Cypress Hills area. But because several small interior drainages in addition to tributaries of the South Saskatchewan, Milk, and Frenchman rivers are all found in this region, it is impossible to relate his data to any specific drainage system.

"Fishing in Alberta" (MacDonald, 1951), "Alberta Sport Fishes" (Anonymous, 1966), and "The Fish of Saskatchewan" (Symington, 1959) all deal with the fishes of these provinces at the popular level but few specific references are made to the Missouri drainage.

The need for a more complete list of the ichthyofauna became more apparent after examining my collections from the Milk and Frenchman river drainages. The number of species contained in these collections was almost double that listed in the available literature. These collections, numbering about 200 and containing some 29,000 specimens, were made during the summer months of 1966 and 1967. A representative collection is deposited in the Royal Ontario Museum, Toronto, Ont. The remainder are in the National Museum of Natural Sciences, National Museums of Canada, Ottawa, Ont.

CHECKLIST

The following checklist is compiled from the collections and the published records previously mentioned. The arrangement follows that of Scott and Crossman's (MS, 1967) checklist.

Species known to be introduced are indicated by an asterisk (*). Those species which are not recorded for Alberta or Saskatchewan outside the Missouri Basin are indicated by a dagger (†), and those species not previously recorded for the Missouri drainage in Canada are indicated by a double dagger (‡).

After the checklist, more detailed species accounts are provided.

CHECKLIST OF THE 27 SPECIES OF FISH FOR WHICH THERE IS A VERIFIABLE RECORD FROM THE MISSOURI DRAINAGE OF CANADA

Salmonidae (5 species)
1. *Prosopium williamsoni* (Girard) — mountain whitefish
††2. *Salmo clarki* Richardson — cutthroat trout
*3. *Salmo gairdneri* Richardson — rainbow trout
*4. *Salmo trutta* Linnaeus — brown trout
*5. *Salvelinus fontinalis* (Mitchill) — brook trout

Esocidae (1 species)
6. *Esox lucius* Linnaeus — northern pike

Cyprinidae (10 species)
7. *Chrosomus eos* Cope — northern redbelly dace
8. *Chrosomus neogaeus* (Cope) — finescale dace
9. *Couesius plumbeus* (Agassiz) — lake chub
*10. *Cyprinus carpio* Linnaeus — carp
†11. *Hybognathus hankinsoni* Hubbs — brassy minnow
12. *Hybognathus nuchalis* Agassiz — silvery minnow
13. *Pimephales promelas* Rafinesque — fathead minnow
14. *Platygobio gracilis* (Richardson) — flathead minnow
15. *Rhinichthys cataractae* (Valenciennes) — longnose dace
16. *Semotilus margarita* (Cope) — pearl dace

Catostomidae (4 species)
17. *Catostomus catostomus* (Forster) — longnose sucker
18. *Catostomus commersonii* (Lacépède) — white sucker
19. *Catostomus platyrhynchus* (Cope) — mountain sucker
††20. *Moxostoma macrolepidotum* (Lesueur) — northern redhorse

Ictaluridae (1 species)
†21. *Noturus flavus* Rafinesque — stonecat

Gadidae (1 species)
22. *Lota lota* (Linnaeus) — burbot

Gasterosteidae (1 species)
23. *Culaea inconstans* (Kirtland) — brook stickleback

Percidae (3 species)
24. *Etheostoma exile* (Girard) — Iowa darter
25. *Perca fluviatilis* Mitchill — yellow perch
26. *Stizostedion canadense* (Smith) — sauger

Cottidae (1 species)
27. *Cottus bairdii* Girard — mottled sculpin

FISHES WHOSE OCCURRENCE IN THE MISSOURI DRAINAGE OF CANADA IS DOUBTFUL OR HIGHLY SPECULATIVE

Ictaluridae
1. *Ictalurus punctatus* (Rafinesque) — channel catfish

Sciaenidae
2. *Aplodinotus grunniens* Rafinesque — freshwater drum

Percidae
3. *Stizostedion vitreum* (Mitchill) — walleye

SPECIES ACCOUNTS

I have compiled the following discussions to provide more precise information on the distributions of these species. However, certain qualifying comments should be kept in mind when reading the accounts.

The major proportion of the Milk River drainage area is located in Alberta. However, several minor tributaries are located in Saskatchewan just east of the border between the two provinces, draining a portion of the Cypress Hills plateau. To avoid any confusion which might arise between species found in these streams and those of the Frenchman River system in the same province, wherever the data are available both the drainage system and the province(s) in which a particular species is found are noted. Unless otherwise noted, records are from the author's collections and the distributions discussed apply only to the Missouri drainage in Canada.

Unless already mentioned in the species account, a chronological listing of those references dealing with the occurrence of each species, specifically in the Missouri drainage of Canada, is given following each species account. Symbols used are the same as those of the checklist.

Prosopium williamsoni — Collected only in the North Fork of the Milk River in Alberta. The mountain whitefish is quite common in this western part of the drainage. (Willock, 1968; Henderson and Peter, 1969.)

††*Salmo clarki* — In the Missouri drainage of Canada, the cutthroat trout, like the mountain whitefish, is limited to the cooler waters of the North Fork of the Milk River.

**Salmo gairdneri* — Recorded only from Horseshoe Lake, a small artificially impounded oxbow in an abandoned meander of the Milk River in Alberta where an original population of 3500 hatchery-reared rainbow trout were planted by the Alberta Department of Lands and Forests in May 1963. Annual plantings have been continued since that date (M. J. Paetz, personal communication). Several other potholes and sloughs in the area also contain artificial and usually nonpropagating populations. Paetz (personal communication) reports the species from Reesor Lake at the head of Battle Creek, a tributary of the Milk beginning in the Cypress Hills. (Willock, 1968.)

**Salmo trutta* — Within the Missouri drainage of Canada, the brown trout is apparently limited to the North Fork of the Milk River (based on author's examination of angler's catch). Its distribution is thus identical to that of the previous two species.

This species was stocked in the Cypress Hills in the late 1920's and early 1930's (Symington, 1959) but I have no knowledge of its occurrence in the Missouri tributaries of these hills. It was known to occur in their South Saskatchewan tributaries. (Scott and Crossman, MS, 1967.)

**Salvelinus fontinalis* — Scott and Crossman (MS, 1967) include the brook trout in the Gulf of Mexico drainage basin on the basis of a specimen from Belanger Creek (E. J. Crossman, personal communication), a tributary of the Frenchman River flowing from Blacker Lake on the eastern edge of the Cypress Hills in Saskatchewan. No specimens were present in my collections.

Esox lucius — Common throughout the Milk River drainage in Alberta. No specimens were obtained from the few locations at which I collected in

the Missouri drainage in Saskatchewan. (Willock, 1968; Henderson and Peter, 1969.)

Chrosomus eos — Present in small, scattered populations throughout the Frenchman and Milk river drainage areas in Saskatchewan and Alberta. (Scott, 1957; McAllister, 1962; Scott and Crossman, MS, 1967; Willock, 1968.)

Chrosomus neogaeus — Scott (1957) records the finescale dace from Lonepine Creek and the Loch Leven outlet stream in Cypress Hills Provincial Park, Saskatchewan. The first stream is a tributary of the Frenchman River whereas the second flows north into the South Saskatchewan via Maple Creek. The author has recorded this species only from tributaries of the Milk to the south and east of the town of Milk River, notably Red Creek and Police Coulee. (Scott and Crossman, MS, 1967.)

Couesius plumbeus — Very common in almost all streams throughout the Missouri basin in Canada. (McAllister, 1962; Scott and Crossman, MS, 1967; Willock, 1968; Henderson and Peter, 1969.)

**Cyprinus carpio* — Atton (1959) reports the occurrence of carp in the Frenchman River as the earliest (1921) acceptable record for this species in Saskatchewan. Carp are as yet unrecorded from Alberta but the possibility of their introduction via a proposed diversion of water from the Marias River into the Milk River in Montana, presumably upstream from Fresno Reservoir, has raised some interest in that province. (Scott and Crossman, MS, 1967; Symington, 1959; McCrimmon, 1968.)

†Hybognathus hankinsoni — Like the northern redbelly dace, the brassy minnow occurs in scattered populations in several of the small tributaries of both the Frenchman and the Milk rivers. The greatest concentration, however, appears to be located in tributaries of both rivers which flow southeastward from the foothills of the Cypress Hills plateau. (Scott, 1957; McAllister, 1962; Scott and Crossman, MS, 1967; Willock, 1968.)

Hybognathus nuchalis — In my previous paper (1968), I reported the presence of the western subspecies of the silvery minnow as the first Canadian record of this subspecies. However, it may be noted that Scott and Crossman (MS, 1967) had previously reported the species, although not by the subspecies designation, from Alberta.

It is known in the Missouri drainage of Canada from only three scattered locations, all in the Milk River east of the town of the same name. Henderson and Peter (1969) report a specimen from the south Saskatchewan River at Medicine Hat. Scott and Crossman's (MS, 1967) record is based on this specimen (E. J. Crossman, personal communication).

Pimephales promelas — Though occurring only as scattered individuals in the Milk River proper because of the relatively swift current and almost complete absence of aquatic vegetation in the stream, the fathead minnow is by far the most abundant cyprinid in all the lesser and more heavily vegetated tributaries of the Milk in both Alberta and Saskatchewan. It is equally common in the Frenchman River and its tributaries. (McAllister, 1962; Willock, 1968; Henderson and Peter, 1969).

Platygobio gracilis — In the Milk River, east of the junction of the north and south forks, the flathead chub is second only to the longnose dace in abundance. West of this junction it appears to be replaced ecologically by the mountain whitefish. Except for the occasional wanderer, it is virtually absent from all the smaller tributaries of the Milk in both Alberta and Saskatchewan. Although Rawson (1949) records this species from the Cypress Hills area, I have obtained no specimens from either the Frenchman River or its tributaries. (Nursall and Lewin, 1964; Scott and Crossman, MS, 1967; Willock, 1968; Henderson and Peter, 1969.)

Rhinichthys cataractae — The longnose dace is common in both larger rivers but, like the flathead chub, occurs infrequently in their smaller tributaries. One exception is the area draining northward from the Sweetgrass Hills, located in Montana just south of the 49th parallel (Fig. 1). The habitat preferences of this species are revealed by its unusual abundance in the swift, gravel-bottomed streams of this region. (McAllister, 1962; Scott and Crossman, MS, 1967; Willock, 1968; Henderson and Peter, 1969.)

Semotilus margarita — Although relatively common in tributaries of the Frenchman River near the Cypress Hills plateau in Saskatchewan, the pearl dace is unknown in the Milk River or any of its tributaries in Alberta. Although no specimens were obtained from the tributaries of the Milk in Saskatchewan, the few collections from these streams are insufficient to verify its absence from that area. (Scott and Crossman, MS, 1967.)

Catostomus catostomus — Young of the longnose sucker are common in most of the tributaries of the Milk River in Alberta, particularly near their mouths. Adults of this species appear to be restricted to the main channel of the Milk. In Saskatchewan, no specimens were obtained from either the Frenchman or the Milk river drainages. (Willock, 1968; Henderson and Peter, 1969.)

Catostomus commersoni — The white sucker is found in large numbers in both the Frenchman and the Milk rivers as well as all tributaries, with the exception of one area. This is the alpinelike habitat found in the upper reaches of streams draining the northern slopes of the Sweetgrass Hills' West Butte. (McAllister, 1962; Scott and Crossman, MS, 1967; Willock, 1968; Henderson and Peter, 1969.)

Catostomus platyrhynchus — Rawson's (1949) record of the mountain sucker in the Cypress Hills area of Saskatchewan may or may not place it in the Missouri basin. My only record from Saskatchewan is a collection from a tributary of Lonepine Creek in the Frenchman River drainage. It is probably present in the Cypress Hills' South Saskatchewan drainage as well. It is common in the west half of Alberta's Milk River drainage.

The most notable populations are those found in the pseudo-alpine habitat of the Sweetgrass Hills. Except for the rumored presence of trout, the mountain sucker may be the only species found in the upper levels of these hills. (Scott, 1957; Willock, 1968; Henderson and Peter, 1969.)

††*Moxostoma macrolepidotum* — The only record of the northern redhorse was 7 miles southeast of Val Marie, Saskatchewan, in the Frenchman River. It was quite common at this station which suggests that the species is present along most of the length of the Frenchman River in Saskatchewan. There is little doubt that it does not occur in the Alberta portion of the Milk River but, as with the pearl dace, the collections from the Milk's tributaries in Saskatchewan are too few to assume it is absent from these streams.

Ictalurus punctatus — Stegner (1955), in "Wolf Willow," a popular account of the early history of southern Saskatchewan, records the occurrence in the Frenchman River of a catfish, "two feet long, his whiskers hung down. his fins and tail were limp — a kind of fish no one had seen in the Whitemud [Frenchman] in the three or four years of the town's life– –." However approximate Stegner's measurements may be, of the three ictalurids recorded by Brown (1962) for the Missouri drainage in Montana, only the channel catfish attains a length of 2 ft.

Richardson (1836, p. 136) gives the type locality for his *Silurus* (*Pimelodus*) *borealis*, a junior synonym of *I. punctatus*, as "Pine-Island Lake, Lat. 54°N," [now Cumberland Lake, Sask.]. F. N. Atton (personal communication) states that: "We have done extensive collecting in the Cumberland lake area and the Saskatchewan River and I feel very sure that this species would have been captured at some time during the last 20 years." There is no valid specimen for Saskatchewan or nearby in Manitoba which casts doubt upon Richardson's type locality.

There are no other records of the channel catfish from Saskatchewan or Alberta. The possibility of its future occurrence there, if indeed it was ever present, is highly unlikely because of a large dam on the Milk, downstream at Fresno Reservoir in Montana, and the numerous smaller irrigation dams present on the Frenchman River.

†*Noturus flavus* — The stonecat has been recorded from only the main channel of the Milk in Alberta; here it is present in moderate numbers in the eastern half of the river. Nursall and Lewin (1964) discuss and qualitatively dismiss the Alberta and Saskatchewan ranges of this species as shown by the range map published by Rostlund (1962). Rostlund's map, which, as noted by Nursall and Lewin, places the species "in the South Saskatchewan River drainage of the southeast corner of Alberta, and the Assiniboine–Red River drainage of Manitoba, with a doubtful distribution between these areas across southern Saskatchewan" was based, for Manitoba, indirectly upon a doubtful record by Bissett (1927) and for Alberta upon an equally questionable record by Eigenmann (1895) who states: "They were reported to me at Medicine Hat, but I did not procure any specimens at that place." (Paetz, 1967; Willock, 1968.)

Lota lota — Present throughout the Milk River in Alberta but no specimens were obtained from the drainage areas of either the Frenchman or the Milk river in Saskatchewan. However, as with the northern pike, its absence from collections gives little reason to assume the nonresidency of as highly tolerant

and widely distributed a species as the burbot. (Nursall and Lewin, 1964; Willock, 1968.)

Culaea inconstans — Although abundant in suitable habitats throughout the Frenchman and Milk river drainages in Saskatchewan, in the much larger Alberta portion of the Milk River system only three widely spread populations were located. Two apparently native populations are located in Mackie Creek and Lodge Creek, both draining southward into the Milk River in the extreme western and eastern portions of the basin. The third population, perhaps the result of an introduction, is in Horseshoe Lake, the artificial trout pond mentioned previously. (McAllister, 1962; Scott and Crossman, MS, 1967; Willock, 1968.)

Etheostoma exile — The presence of the Iowa darter was based on the sporadic occurrence of small numbers in three tributaries of the Milk River in Alberta. Two of these approach the river from the south whereas the third, Lodge Creek, arises in the Cypress Hills area of Alberta and flows southeastward through Saskatchewan before joining the Milk in Montana. In the Frenchman River drainage it appears to be limited to the upper stretches of those tributaries arising in the Cypress Hills region. (McAllister, 1962; Willock, 1968.)

Perca fluviatilis — Although quite common in the main channel of the Frenchman River, no specimens of yellow perch were taken from the Milk River drainages of either Saskatchewan or Alberta. M. J. Paetz (personal communication) reports 56,000 fingerlings planted in Shank's Lake, Alberta, in August 1960. (Scott and Crossman, MS, 1967.)

Stizostedion canadense — The sauger is distributed along the entire length of the Milk River in Alberta. Its population equals or surpasses that of the northern pike, the other large predator and game fish of the area. I know of no record of its occurrence in the Frenchman River drainage of Saskatchewan. (Anonymous, 1966; Paetz, 1967; Willock, 1968; Henderson and Peter, 1969.)

Stizostedion vitreum — No specimens were present in the author's extensive collections from the Milk River; however, it is mentioned as occurring in the Milk River in "Alberta Sport Fishes," (Anonymous, 1966). This locality is probably based on an angler's report and results from misidentification of a sauger (M. J. Paetz, personal communication). The walleye has been collected from Fresno Reservoir in Montana (R. G. Needham, personal communication).

Aplodinotus grunniens — The only published record of the freshwater drum, from Alberta or Saskatchewan, is one by Atton and Johnson (1955) which consisted of "two dead specimens found on the bank of Swiftcurrent Creek at Swift Current on June 12, 1953." Brown (1962) reports this species from the Missouri River in Montana and Rostlund (1952) repeats a record from the Milk River, in the same state, originally given by Evermann and Cox (1894).

The first record above is from the South Saskatchewan drainage and thus cannot be included in a checklist of the Missouri drainage of Canada.

However, the possibility of its occurrence in the Frenchman River drainage in the past, if not at present, should not be overlooked.

Cottus bairdi — Specimens of the mottled sculpin which, according to D. E. McAllister (personal communication), closely resemble the form found in the Cordilleran foothills of Montana, are common in collections from the North Fork of the Milk River. This species was not collected elsewhere in the Canadian portion of the Missouri basin.

In conclusion, about 200 collections containing some 29,000 specimens were made in the Milk and Frenchman river drainages. Twenty-seven species are known to occur in the Canadian portion of the Missouri drainage and three additional species may have been present there. Of these 27 species, 23 are recorded from the Milk River drainage and 15 from the Frenchman River drainage. Of the 12 species included in my collections from the Frenchman River drainage (*Chrosomus eos*, *Couesius plumbeus*, *Hybognathus hankinsoni*, *Pimephales promelas*, *Rhinichthys cataractae*, *Semotilus margarita*, *Catostomus commersoni*, *Catostomus platyrhynchus*, *Moxostoma macrolepidotum*, *Culaea inconstans*, *Etheostoma exile*, and *Perca fluviatilis*) definite records from this drainage were previously published for only the northern redbelly dace and the brassy minnow.

By far the greatest number of collections were from the Milk River drainage and it can be said, with some degree of certainty, that *Cyprinus carpio*, *Semotilus margarita*, and *Moxostoma macrolepidotum*, all found in the Frenchman River drainage, do not occur in the Milk River drainage of Alberta. However, only nine collections containing 716 specimens were taken from the Frenchman River drainage, a number too low to suggest that the list of species from that area is complete.

Salmo clarki and *Moxostoma macrolepidotum* are added and it is suggested that *Stizostedion vitreum* be omitted from the list of Canadian Missouri drainage fishes.

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Histology and Fine Structure of the Accessory Boring Organ of *Polinices lewisi* (Gastropoda, Prosobranchiata)

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The histology of the accessory boring organ of the naticid clam drill *Polinices lewisi* (Gould) was investigated by means of electron microscopy and standard histological techniques.

The organ consists of two distinct epithelial regions, one producing typical mucin histochemical reaction and a central region which secretes a proteinaceous substance. Overlying the central epithelium is a brush border consisting of numerous microvilli passing through a matrix of protein and chitin.

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INTRODUCTION

A NUMBER OF GENERA of carnivorous marine prosobranchs of the order Mesogastropoda, notably the Muricidae and Naticidae, possess the ability to drill the shells of other molluscs. That drilling is not always limited to calcareous exoskeletons was noted by Thorsen (1935), who reported drilled egg capsules of the gastropod *Sipho* and by Jensen (1951) and Ansell (1961), who found elasmobranch egg cases similarly pierced.

Debate has surrounded the means of penetration, two schools of thought arising; the one hypothesizing radular action and the other chemical attack upon the prey's shell. Reaumur (1711) first suggested the chemical theory and was supported by Schiemenz (1891) who noted that the secretion from the papilla described by Troschel (1854) reddened litmus paper. Hirsch (1915) showed that the diameters of the accessory boring organ and the resultant hole were identical and assumed one was made by the other. Ankel (1937) reported that the excised organ from *Natica* etched the surface of a *Trivia* but subsequently (1938) failed to obtain etching and postulated the presence of an enzyme "calcase" active only under optimum conditions.

Fischer (1922) considered the naticid accessory boring organ to be primarily a muscular structure poorly supplied with glands. This upheld the view that drilling was accomplished by radular abrasion and this idea was further supported by Loffens (1926). Ziegelmeire (1954) also contended that penetration is simply mechanical.

The situation is more complex than a simple acid-secretion, vs. radular abrasion system of penetration. Turner (1953) demonstrated the ability of

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Polinices duplicatus to perforate shells of *Mya arenaria* which had first been coated with histological paraffin wax or with calcium sulphate. Carriker (1959) considers that an alternation of chemical and mechanical means is employed. This view was strengthened (Carriker, 1961) by a study of electron micrographs of muricid accessory boring organ etchings, clearly showing that the surface crystals of shell calcite, and also inorganically deposited calcite and aragonite crystals, are softened and loosened, to be easily removed by the radula.

Excellent reviews of the literature are given by Carriker (1961) and Carriker et al. (1963). However, most attention has been given to the readily accessible accessory boring organ of the Muricidae, which is situated on the foot. Fretter and Graham (1962) give a drawing of the histology of the naticid boring organ; however, little is known of the function and anatomy of this structure.

Polinices lewisi (Gould), a large naticid predator on clams, was the subject of this study. For brevity, the term "accessory boring organ" is abbreviated to ABO.

MATERIALS AND METHODS

Material must be fixed with the proboscis fully extended, otherwise the ABO forms a highly convoluted mass projecting into the lumen of the false mouth. Various relaxants were unsuccessful and best results were obtained as follows.

The shell is removed and the propodium cut away, exposing the cephalic region. The proboscis is drawn forward with forceps and a loose ligature placed around the posterior portion of the buccal mass. Pressure on the cephalic sinus causes the proboscis to be fully everted and the ABO to become turgid. The ligature is tightened and the entire proboscis excised and placed, still ligatured, in the fixative. After fixation the ABO is dissected from the proboscis.

For electron microscopy, small blocks of fresh ABO were fixed in cold 4% glutaraldehyde in phosphate buffer (*p*H 7.4) for 2 hr, then postosmicated prior to dehydration and embedding in Epon resin; sections were then stained in uranyl acetate. For routine histological examination, specimens were fixed in formalin–aceto-alcohol (5, 5, 90 ml 70%), and 5 - μ section swere stained using four techniques: (i) Chitosan test for chitin (Campbell, 1929); (ii) Periodic Acid Schiff and Light Green for polysaccharides (MacManus, 1948); (iii) Lillie's Allochrome for connective tissue (Lillie, 1951); (iv) Thionin stain at *p*H 5.0 for mucin (Highman, 1945).

OBSERVATIONS

General Morphology

When contracted the ABO of *P. lewisi* appears as a shapeless mass of tissue attached to the lower lip of the acrembolic proboscis and filling a portion of the annular lumen of the false mouth. In this condition it is difficult to note any relationship among the tissues and this probably led to Fischer's (1922) conclusion that the organ was solely muscular. When the proboscis is everted the ABO is capable of great tumescence and then appears as a fungiform papilla with a diameter equal to that of the proboscis.

In vertical section the erect ABO is a fungiform papilla joined by a short peduncle to the ventral distal tip of the proboscis. Examination of sections of the entire organ stained by orthodox methods reveals distinct regions: (*a*) the central area consisting of tall columnar epithelial cells bearing an

amorphous cuticular layer variously interpreted as a "cuticle" (Ziegelmeier, 1954) or "rodlet border" (Fretter and Graham, 1962); (*b*) the lateral raised portion of the ABO and peduncle is covered with cylindrical nonciliated epidermal cells containing many gland cells; (*c*) a lateral ring of subepidermal mucocytes; and (*d*) the inner body of the ABO is composed of mesenchymatous cells, muscle and collagenous fibres, blood vessels, and large sinusoidal spaces with numerous muscle fibres extending from the inner regions of the peduncle to the proximal ends of the central epithelial cells (Fig. 1).

Tumescence of the ABO is the result of engorgement of the circumproboscidal sinus (Bernard, 1967) which communicates with the central lumen of the ABO via the peduncle. Control of turgescence appears to be maintained by the bands of circular muscle in the peduncle. A large branch of the buccal artery supplies the ABO, forming a rich network on the proximal ends of the central tall epithelial cells. Little nerve tissue is present and no sensory areas were observed. This does not uphold Ziegelmeier's (1954) hypothesis that the ABO is a tactile organ monitoring the performance of the radula in piercing the prey's shell.

The central cuticle (Fig. 1) is easily stripped away from the underlying cells. Because of its amorphous appearance under light microscopy and its superficial similarity to the bivalve gastric cuticle, the standard test for chitin, involving its conversion to chitosan, was applied to pooled material stripped from the central region of a number of ABOs. Positive coloration was obtained although the reaction was faint. The mechanism of Campbell's Chitosan test is not understood, but a positive reaction is considered specific for chitin. Hackman (1964) has pointed out that there are no histochemical tests for chitin present in delicate structures in microtome sections.

Sections demonstrated two distinctly differentiated epithelial areas and subdermal pockets of large mucocytes, supported by a body of mixed connective tissue and large intercellular lumina (Fig. 1). The central epithelium is composed almost exclusively of elongate goblet cells with granular cytoplasm and medially situated nuclei. The distal borders of these cells present a striated appearance and bear an amorphous layer of acidophilic material. The cytoplasm of individual cells contains large vacuoles in which are evident irregular networks of basophilic strands. Individual goblet cells are not joined except at their distal extremities where pockets of secreted material are present just below the cuticle (Fig. 2A).

The lateral covering of the ABO consists of an epithelial layer composed of cylindrical cells and many mucocytes. The junction of the "cap" and peduncle is thrown into deep invaginations. The lateral epithelial cells show less affinity for the acid counterstain, but contain a large proportion of deeply staining basophilic material. This lateral covering is similar to the dermal layers of the upper surface of the foot, but lacks the ciliation. Of particular interest is that the lateral epithelium, as expected, stands on a well-defined basement membrane, but this is lacking under the central epithelial cells which are in direct communication with the blood vessels and other tissues of the central body of the ABO (Fig. 2B).

A ring of subdermal mucocytes surrounds the central epithelial layer. These cells consist of five or more clustered cells surrounded by strands of connective tissue (Fig. 2B). The situation is similar to that existing in the pedal gland of *Arion rufus* (Linné) described by Chetail and Binot (1967).

The deep layers of the ABO consist mainly of large aquiferous spaces, bridged by muscle fibres and connective tissue fibrils, stellate cells, and numbers of amoebocytes.

Using Periodic Acid Schiff (PAS) with light green, the sections demonstrated scattered globules of PAS-positive material concentrated in the proximal region of the central epithelium and in the outer free cell borders. The cuticle layer is faintly positive. The lateral epithelial cells and subdermal mucocytes are also positive. Glycogen is not responsible for the positive result as a diastase control did not alter the reaction.

The central epithelium is not uniformly coloured by the Lillie's allochrome, most of the cells being greenish in their proximal portions, graduating to bluish-purple at the distal extremities. The superficial cuticle appears faintly banded blue and reddish-purple. The lateral epithelium and subdermal mucocytes are stained a uniform pink. Scattered throughout the central connective tissue and in the interstitial pockets of the central epithelium are granules staining bright red. The central portions of the ABO cap and the peduncle display the typical prosobranch musculature and blood sinuses (Fig. 1).

Highman's (1945) thionin staining was modified by use at *p*H 5.0 and an acetate buffer substituted, as phosphates precipitated the thionin. The central epithelial cells stained light blue and the nuclei black. Many cells showed large clear vacuoles containing a faintly stained network of fibres. The lateral epithelium was only lightly stained, but interstitial goblet cells with long necks reaching to the surface were deep purple. In some areas quantities of deeply stained substance had broken to the surface. The subdermal cell pockets appear a bright purple situated in a lighter staining network of connective tissue.

Electron Microscopy

The cuticle is composed of microvillar prolongations of the central epithelial cells. The sections in Fig. 3B are not vertical so the microvilli are in tangential section. There is considerable amorphous matter between individual microvilli, but these extend to the outer surface (Fig. 4A). In more lateral areas the microvilli become detached from the underlying cells, but it is not clear if this is the result of preparation or lesions caused by excision of the EM blocks (Fig. 3A).

The central epithelium consists of a single layer of elongated cells. The proximal ends are considerably infolded and bear intimate relationship to the tissues of the central body of the ABO; no true basement membrane could be discerned. At their distal extremities, adjacent cells are connected by terminal bars (Fig. 3C). The medially situated nuclei are associated with fine granular bodies which appear to bear some relationship to Golgi complexes. Large

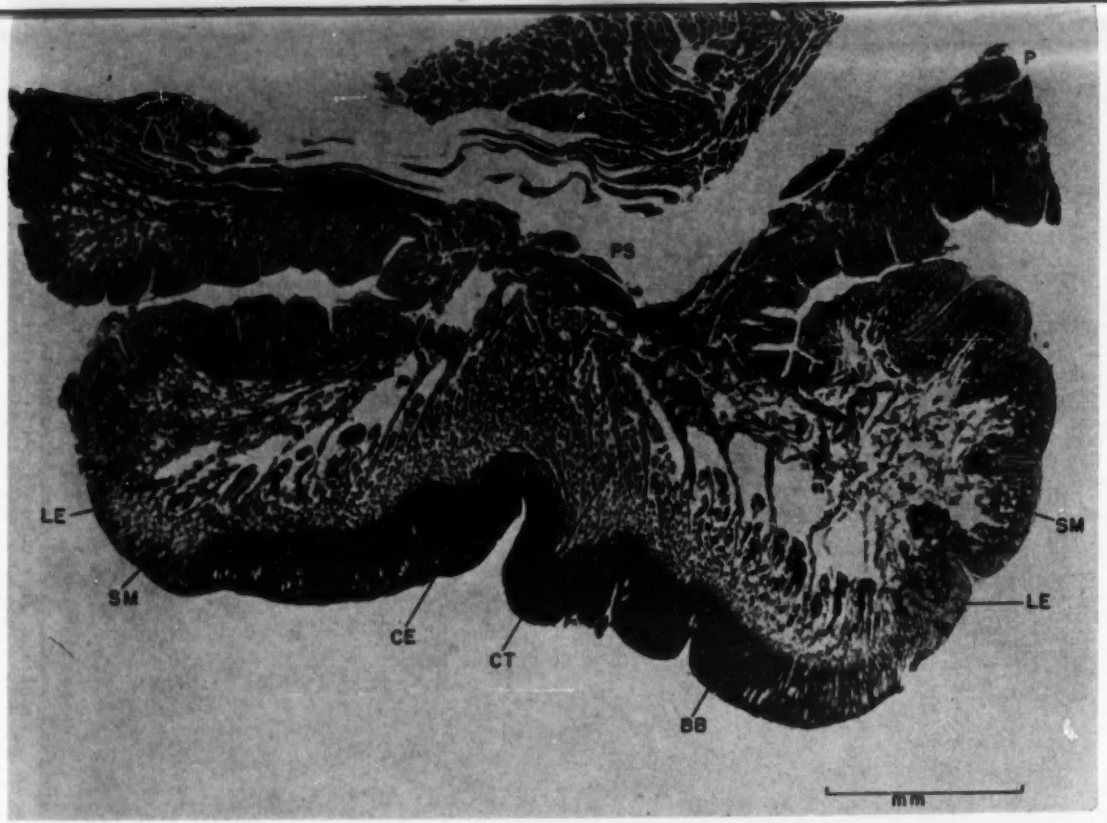

FIG. 1. Median sagittal section of entire accessory boring organ of *Polinices lewisi*. Stained by Lillie's Allochrome. BB = brush border; CE = central epithelium; CT = connective tissue; LE = lateral epithelium; P = proboscis; PS = proboscidal sinus; Ped. = peduncle; SM = subdermal mucocytes.

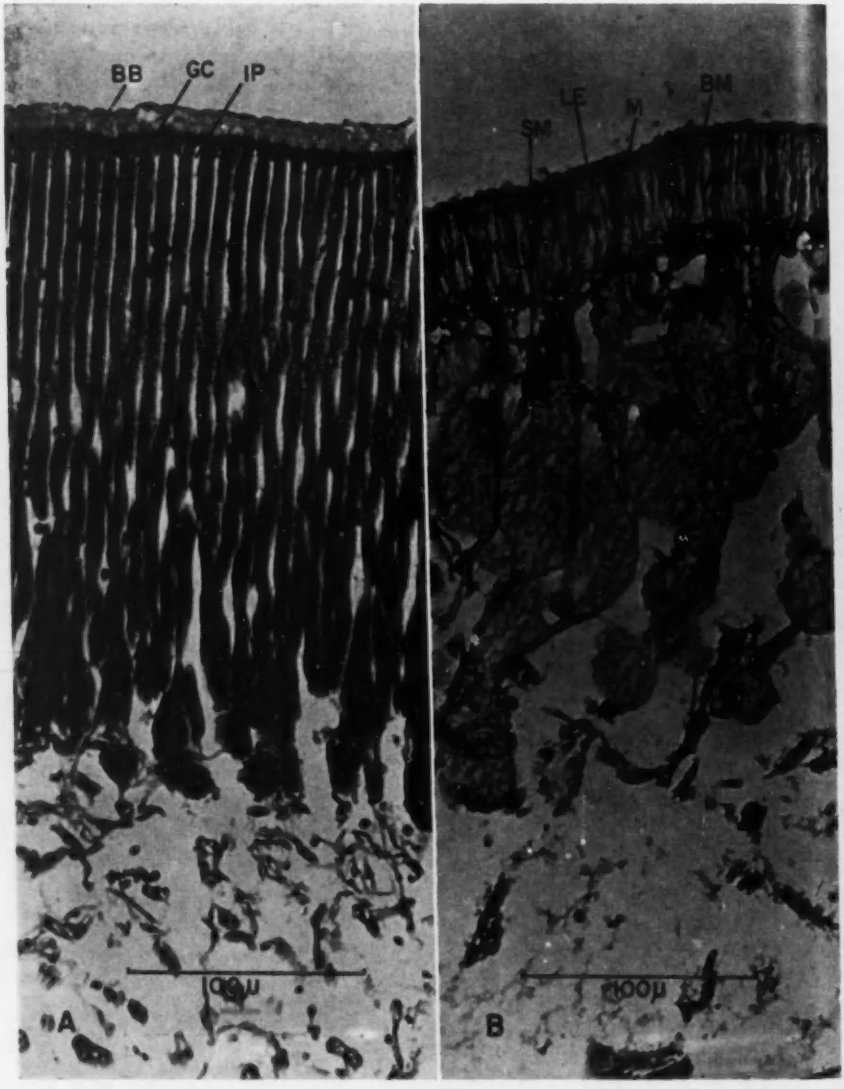

FIG. 2. (A) Central epithelium; BB = brush border; GC = goblet cell; IP = interstitial pocket. (B) Lateral epithelium and subdermal mucocytes. BM = basement membrane; LE = lateral epithelium; M = mucocyte; SM = subdermal mucocytes.

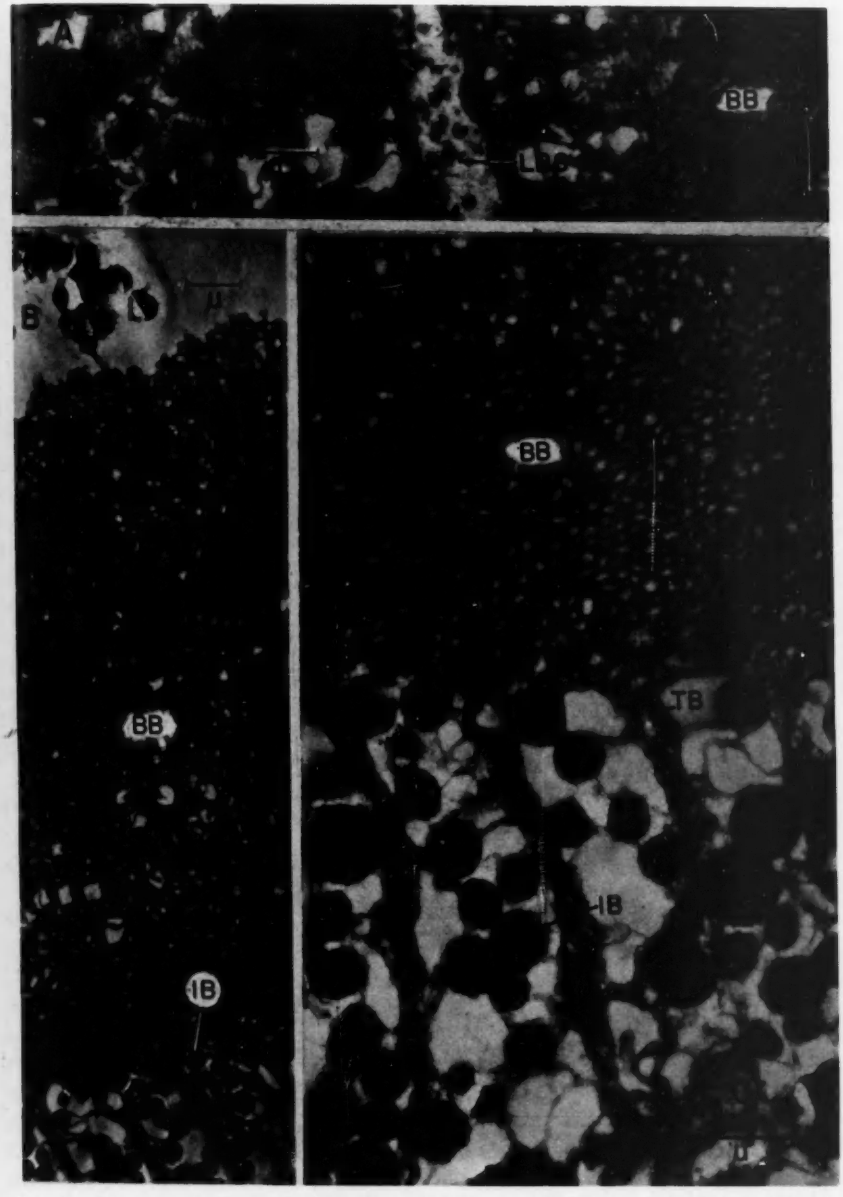

FIG. 3. Electron micrographs of the accessory boring organ of *Polinices lewisi*. (A) Brush border on lateral portion of central epithelium. BB = brush border; LBS = lateral basal space. (B) Section through brush border and distal portions of columnar goblet cells. BB = brush border; IB = inclusion body. (C) BB = brush border; IB = inclusion body; TB = terminal bar.

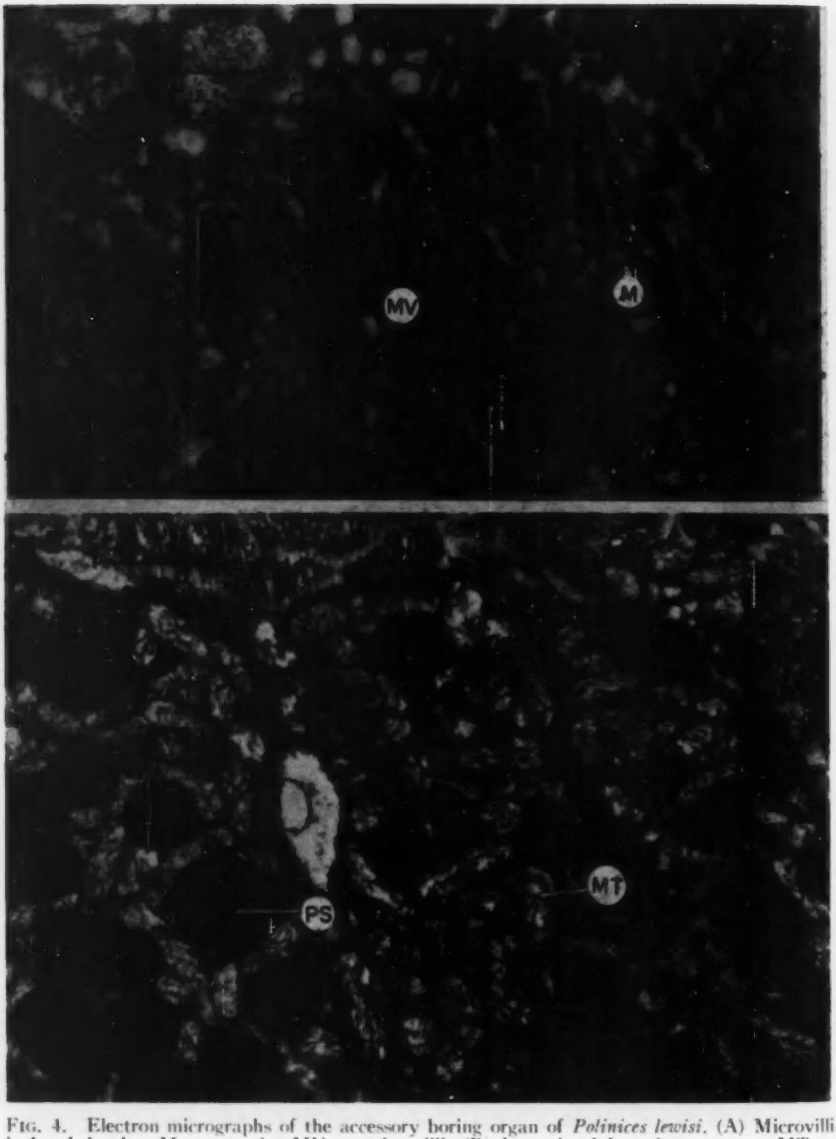

FIG. 4. Electron micrographs of the accessory boring organ of *Polinices lewisi*. (A) Microvilli in brush border. M = matrix; MV = microvilli. (B) Lateral subdermal mucocytes. MT = mitochondrion; PS = pigment sphere.

inclusions, similar to the "pigment spheres" described in the lamellibranch digestive system by Owen (1958) are present. These inclusions are most numerous in the proximal portion of the cells but probably migrate to the distal region. They are densely shadowed, probably of a lipid nature because of their ready uptake of osmic acid.

The subdermal mucocytes contain similar inclusions but these are composed of dense granular and lamellated structures. Also present are clusters of small lipid spheres. Mitochondria are associated with the inclusions (Fig. 4B).

DISCUSSION

The study of stained sections clearly demonstrates the distinctiveness of the central epithelium from the lateral epithelium and the subdermal mucocytes. The central area with its large goblet cells and general structure is suggestive of a serous epithelium. Of particular interest is the apparent lack of a basement membrane at the intimate connection of the central cells to the underlying vascular and sinusoidal system. The lateral epithelium is homologous with the rest of the dermal layer of the snail's body but lacks ciliated cells. The subdermal cell clusters produce an acid mucopolysaccharide and are analogous to the pedal mucous gland of many prosobranchs. These originate as simple goblet cells which have migrated inwards and become arranged in subepithelial groups.

The Schiff reaction points to the subdermal and lateral epithelial goblet cells secreting an acid mucopolysaccharide, and the central area probably secretes a mucoprotein. The metachromia of thionin clearly demonstrates that mucin is elaborated only by the lateral goblet cells and the subdermal mucocytes.

The main function of the subdermal mucocytes, which form a ring around the central epithelium underlying the convoluted lateral epithelium and discharge at the edge of the cap of the ABO is probably to provide a lubricant or "seal" when the ABO is applied to the shell surface.

Light microscopy of the brush border reveals little structure, but electron microscopy has shown that numerous microvilli are present in an amorphous matrix, probably consisting of protein and small amounts of chitin.

This study supports the suggestion of Fretter and Graham (1962) that the central epithelium bears a "rodlet" border capable of passing enzymatically active material. Carriker et al. (1967) reported that when in use the *p*H of the ABO in *Urosalpinx* drops to 3.8, indicating the presence of an uncharacterized acid, though enzymes and chelating agents may also be present. Person et al. (1967) have shown that cytochrome oxidase, succinate dehydrogenase, and lactate dehydrogenase activities are localized in the central epithelial cells.

An important paper by Halton and Owen (1968) clearly demonstrates that the so-called "inert cuticle" of the protobranch bivalve *Nucula sulcata* (Bronn) is enzymatically active and is composed of microvilli in a chitinous matrix. The similarity to the cuticle of the naticid ABO is striking and raises

many interesting speculations concerning the origin and function of enzyme secretory and digestive processes within the Mollusca.

A short descriptive note by Provenza et al. (1966) suggests a striking histological similarity between the naticid and muricid ABO. The ABO in Muricidae was first described by Fretter (1941), who considered it a pedal sucker (Fretter, 1946). Carriker (1943), apparently unaware of Fretter's paper, described the structure and correctly noted its intimate relationship with prosobranch shell drilling and surmised that it secreted a shell-softening substance. The development of such similar organs on different parts of the body is one of the most interesting parallels in molluscan morphology.

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Quantitative Comparison of Peritoneal Washes and Feces for Detecting Infectious Pancreatic Necrosis (IPN) Virus in Carrier Brook Trout

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BILLI, JAMES L., AND KEN WOLF. 1969. Quantitative comparison of peritoneal washes and feces for detecting infectious pancreatic necrosis (IPN) virus in carrier brook trout. J. Fish. Res. Bd. Canada 26: 1459–1465.

Paired fecal samples and peritoneal washes were taken from 300 18-month-old brook trout for determining their relative value in detecting IPN virus. The testing of feces revealed 14 times as many carriers as were found by peritoneal washes. Initial examinations showed at least 63% of the fish to be carriers of the virus, but 30% more were detected in four additional tests. Fecal output of virus from 37 fish was quantified up to five times during a period of 7 months which included the spawning season. Although there were exceptions, fish with high outputs of virus tended to maintain that level, and low titer carriers tended to yield small amounts, and in some instances, no virus. Tests of fecal extracts which were pooled from 5, 10, and 15 fish showed that virus was readily detected in all three. For economy and efficiency, the use of 10- or 15-sample pools is recommended for determining the presence of IPN in fish.

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INFECTIOUS PANCREATIC NECROSIS (IPN) is an acute viral disease of trout which typically causes high mortality among the young. The disease, detection, isolation, and identification of the virus, and methods of control have been described recently (Wolf and Quimby, 1968; Wolf et al., 1968). Some fish survive the disease but retain the infection and become carriers, possibly for life. Transmission occurs by contact, probably through ingestion, and from parent stock via the eggs. Since there is no therapy, effective control is accomplished presently by preventing exposure to the pathogen. This is achieved by obtaining fertile eggs, or offspring, from virus-free broodstock and propagating them, at least through the susceptible-to-disease stage, in a virus-free environment. Where environments are known to be free of IPN virus, measures must be taken to prevent its introduction. In order to determine whether a particular population is free of virus, or to select virus-free individuals from a population which harbors carriers, it is necessary to examine fish for the presence of virus. For this purpose populations or production lots of fish have been examined by testing suitable numbers of pools of peritoneal washings or fecal extracts prepared from five fish (Wolf and Quimby,

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1968). Larger numbers of fish for each pool would require fewer materials and less work. If virus could be detected dependably in larger pools, the sample size could be increased and there would be a greater probability of detecting IPN virus carriers if such were present.

Since transmission of the disease is likely to occur by means of infected fertilized ova, prevention (of transmission) can best be achieved by obtaining eggs and sperm from IPN-free broodstock. The purpose of this report is to compare methods of detecting IPN virus in broodstock.

The objectives of this experiment were: (1) to establish the comparative value of fecal samples and peritoneal washes as source material for detection of IPN virus; (2) to determine the relative value of 5-, 10-, and 15-fish pools of material in such work; (3) to quantify periodically the IPN virus in known carrier brook trout (*Salvelinus fontinalis*) and determine if fluctuations in virus level occur; (4) to determine whether noncarriers remained noncarriers.

In a test using peritoneal washes at the White Sulphur Springs National Fish Hatchery (Wolf et al., 1968), a 10% sample of 2900 rainbow trout (*Salmo gairdneri*) showed a 0.3% incidence of IPN carriers. One month later, 50% of the same population was tested using (aliquots of) 5-fish pool samples of feces to compare with 5-fish pool samples of peritoneal washings. Assuming that each detection of virus represented at least one carrier, examination of feces gave an estimate of infection of at least 6.8% of the population whereas tests of peritoneal washes showed at least 1.6% of the fish to be carriers.

A preliminary test, at the Eastern Fish Disease Laboratory, Kearneysville, West Virginia, of 40 brook trout, also indicated that fecal sampling was a more sensitive test. Virus was found in six of eight 5-fish fecal pools, but virus was not found in any of the pooled peritoneal washes from the same fish. Virus was found in three of four pools when portions of the fecal samples were combined into 10-fish pools.

MATERIALS AND METHODS

Source of Fish and Identification of Individuals

Three hundred 18-month-old brook trout were obtained as a representative sample from a single production lot at the Leetown National Fish Hatchery, Kearneysville, W.Va. The fish originated as eggs from stock at the Edray, W.Va., state fish hatchery, and had been held in the same raceway for a year prior to this work. They were survivors of an IPN epizootic. Virus was isolated from them and identified by serum neutralization (Wolf et al., 1968) to be IPN virus. The fish were tagged with individually numbered disc tags, and kept in a single tank in water, the properties of which have been reported elsewhere (Warren, 1963).

Cell Culture

Cells used in this experiment were rainbow trout gonad (RTG-2) from 52nd to 141st subculture. Cells were dispersed with a mixture of 1: 5000 versene and 0.1% pancreatin, and grown in Eagle's Minimum Essential Medium (Earle's Balanced Salt Solution (BSS)), plus 10% fetal bovine serum. The medium contained 100 μg streptomycin, 100 units of penicillin and 25 units of nystatin per ml.

Static 16 × 150 mm culture tubes were seeded with 1 ml of cell suspension and inoculated 1–4 days later while cultures were still young and active but confluent, about 275,000 cells per

ml (J. Plumb, 1967, personal communication). Inoculant volume was 0.1 ml throughout this work. Cultures were incubated at 18–25 C and examined every day for 7 days.

Method of Sampling

Initial survey — The fish were anesthetized with 25 ppm quinaldine. Samples of feces (0.5 ml) were measured by collecting the material in tubes which held 4.5 ml of sterile Hanks' BSS and which were calibrated at 5 ml. The samples were shaken vigorously and allowed to settle for 1–2 hr; then the supernatant fluid was removed, filtered through a Swinney adapter with a Millipore HA (450 mμ) membrane, and inoculated into cultures.

For peritoneal washes, a ventral surface site on the fish was disinfected with 70% isopropyl alcohol, and 5 ml of sterile Hanks' BSS were injected into the body cavity. The fish was massaged to suspend and collect virus, and then at least 2 ml were withdrawn and put into a tube. The peritoneal wash was also filtered through a Millipore HA membrane.

Specimens from every fish were examined individually, then portions of individual samples were combined into 5-, 10-, and 15-sample pools.

Repeat surveys — Fish which showed no virus in the initial survey were tentatively considered to be noncarriers; they were re-surveyed, but only fecal samples were taken. Those which showed no virus in the second test were examined a third time, and if they were still without virus, they were examined a fourth time.

Confirmation — IPN virus-caused cytopathic effect (CPE) in RTG-2 cells is lytic and severe, but similar CPE can be caused by unidentified toxic materials present in fecal extracts. Therefore, a fish was considered to be a carrier only if medium from affected cultures produced CPE upon transfer to fresh RTG-2 cultures.

Quantification of Virus in Carrier Fish

Virus was quantified in both feces and peritoneal washes from carrier fish. Samples were filtered through a HA membrane, serially diluted in 10-fold steps to 10^{-6}, and inoculated into cell cultures. Five culture tubes were used for each dilution. The 50% infectivity endpoint was determined by the Kärber method (Rhodes and van Rooyen, 1953).

Thirty-seven of those fish whose fecal samples yielded virus were resampled periodically (five times) and titrated. Only one titration was carried out on the seven peritoneal washes that yielded virus.

RESULTS

Comparison of Feces and Peritoneal Washes as Sources of Virus

In the initial survey, 63.3% of the individual fecal samples and 4.7% of the peritoneal washes yielded virus. These results showed the superiority of feces as test material for viral detection and clearly indicated the method to be employed for the balance of the work.

Among those fish which had been negative on the first examination, 56.3% (62 fish) yielded virus on second fecal sampling. A third sampling showed 18 of the remaining 48 fish (37.5%) to be positive. The fourth screening detected 8 additional carriers and left only 7.3% (22 fish) of the original 300 fish to be considered noncarriers.

In the initial survey, 190 carriers were detected using fecal samples. Fourteen carriers were detected by using peritoneal washes, only three of which had not been detected by using feces. Considering only the initial examination, tests of feces detected 190 of the 193 determined carriers, for an efficiency of 98.4%, whereas peritoneal washes revealed 14 fish or 7.2% of the known carriers.

Of the cultures 5% showed CPE which did not transfer; therefore, the CPE was attributed to toxicity or other nonviral factors.

Relative Value of Pooled Samples in Virus Detection Work

In the peritoneal washes, only 1 of the 5-fish pools and 1 of the 10-fish pools was positive. These contained one positive trout. The 15-fish pool containing material from this trout showed no viral CPE.

Fifty-six of 60 5-fish pools of fecal material were positive, 28 of the 30 10-fish pools were positive, and 18 of 20 15-fish pools showed virus.

When the data were organized according to increasing number of carriers in each pool of feces, it was found that virus was not detected in some 5-fish pools which had but one or two carriers. On a percentage basis, 5-, 10-, and 15-fish fecal pools all showed about the same incidence of carriers in the population, 90–93% (Table 1).

Table 1. A comparison of test efficiency using fecal pools of different sizes for detection of IPN virus.

No. of carrier fish in each pool	No. of fish used for each pool of feces		
	5-fish pool	10-fish pool	15-fish pool
1	2/3[a]	–	–
2	9/12	–	–
3	22/22	1/1	–
4	18/18	3/3	–
5	5/5	5/5	1/1
6		4/5	–
7		10/11	1/2
8		2/2	3/4
9		3/3	3/3
10		–	2/2
11			5/5
12			2/2
13			1/1
14			–
15			–
%	93.3	93.3	90.0

[a]Numerator indicates the number of samples which showed virus and the denominator indicates the number of samples tested.

Quantification of Virus in Feces and in Peritoneal Washes

The amount of virus present in feces from individual fish ranged from a low of $10^{1.7}$ to $10^{7.5}$ ID_{50} (Table 2). Successive titrations showed that most but not all carriers shed virus each time they were sampled. The virus titer of individual fish tended to remain at a high level if it was high at the time of the first test. The quantity, however, was remarkably uniform; the average

TABLE 2. Virus content of feces from individual fish during a period of 9 months.

Fish no.	Titration 1st	2nd	3rd	4th (pre-spawning)	5th (post-spawning)
1	2.3[a]	Died			
2	4.9	4.2(38)[b]	4.8(88)	5.5(163)	5.5(243)
3	1.7	3.5(38)	4.1(88)	2.8(106)	0(230)
4	0	1.9(44)	0(88)		0(171)
5	2.1	5.3(38)	Died		
6	1.9	2.5(38)	3.1(88)	2.5(178)	0(275)
7	1.9	3.3(38)	2.5(88)	0(163)	0(171)
8	3.7	5.9(31)	Died		
9	3.9	5.3(31)	4.5(81)	4.6(171)	3.5(223)
10	4.7	5.1(31)	2.5(81)	5.1(171)	0(223)
11	2.5	4.1(35)	3.5(81)	5.8(155)	5.8(235)
12	5.3	5.5(81)	5.8(81)	Died	
13	4.9	5.1(35)	0(81)	5.5(171)	
14	4.1	4.9(27)	4.5(72)	5.5(162)	3.5(139)
15	4.9	7.5(27)	4.1(72)	6.1(162)	3.5(139)
16	5.3	4.7(32)	6.8(76)	6.5(166)	
17	1.9	3.1(27)	0(72)	0(148)	0(228)
18	5.3	6.1(27)	5.5(72)	6.1(162)	5.1(229)
19	4.5	4.5(27)	4.8(72)	4.5(93)	Died
20	4.3	4.3(23)	3.8(66)	7.5(104)	Died
21	5.3	5.1(21)	Died		
22	5.5	3.7(23)	4.5(66)	5.8(156)	0(223)
23	5.3	2.5(23)	Died		
24	4.9	4.5(23)	4.8(66)	5.1(156)	0(223)
25	4.9	5.1(21)	4.8(66)	2.8(142)	0(222)
26	1.9	2.7(23)	0(66)	0(142)	1.8(222)
27	4.7	4.7(9)	4.5(60)	1.8(164)	Died
28	2.9	2.7(9)	4.1(53)	1.8(128)	2.1(208)
29	4.9	4.3(9)	3.8(53)	2.8(157)	0(210)
30	5.1	4.9(9)	3.8(53)	3.5(157)	0(210)
31	5.1	5.3(9)	4.5(53)	4.8(157)	2.1(210)
32	2.7	1.9(9)	0(53)	Died	
33	5.9	5.9(9)	4.5(53)	0(157)	3.1(210)
34	0	Died			
35	0	0	0	Died	
36	3.1	Died			
37	2.1	Died			
Avg	3.6	4.2	3.3	3.8	1.7

[a]Exponent of $\log_{10}$ of the ID_{50} per ml.
[b]Figures in parentheses indicate number of days from first titration.

amount of virus for the first titration was $10^{3.6}$ ID_{50} per ml, the average for the second was $10^{4.2}$, the third titration was $10^{3.3}$, and the fourth was $10^{3.8}$. The fifth (or post-spawning) titration was lower, $10^{1.7}$, due to many of the samples being negative.

Fish used in the titrations of peritoneal washes had been positive in the initial survey but at the time the seven were titrated, five proved to be negative, one had a titer of $10^{4.3}$, and the other, $10^{1.3}$ ID_{50} per ml.

DISCUSSION

After five screenings, 92.7% of the 300 fish were shown to shed IPN virus at one time or another; this is the highest incidence of carriers yet encountered, but it must be emphasized that this surprising percentage is actually a cumulative value. If the complete lot had been tested each time, the average estimated indicence at any single time could be comparable with the 63% found on initial survey. As an example, using only the results of the fifth titration (Table 2), the estimated carrier incidence is less than 50%. In any event, the results point out the need for repeated careful testing when it is necessary to have absolute assurance that particular fish are free of IPN virus.

We do not know what effect, if any, tagging and handling had on the incidence of carriers. In the absence of firm evidence to the contrary, we recognize the possibility that the manipulations conceivably might have contributed to an increase in the number of carriers. We are, however, much more inclined to believe that tagging and handling were not significant factors, and there is evidence to support this belief. The sample of 300 fish came from a production lot in a facility with a long history of IPN. As such, the fish probably had been exposed to virus for the first time during the epizootic which gave rise to the carriers with which we worked. Secondarily, the carriers shed virus so that in all probability all fish were exposed frequently if not continually during the 18 months which preceded our work. Furthermore, we have recently found that when brook trout encounter IPN virus for the first time as adults, they become infected but show no disease. Such fish mount a strong immune response and are able to clear themselves of virus completely (unpublished research).

At the time of each titration there were individual fish from which we did not get measurable quantities of virus. Among the first four measurements, the percentage of "negative" fish was generally low — from 3 to 20%, but on the fifth and last titration we failed to detect virus in slightly more than half the fish tested. We do not know the reason for the change, but the occurrence suggests that a temporal reduction in virus output might have been involved.

In this study, the 5-, 10-, and 15-fish pools of fecal extracts gave comparable results in qualitative detection of IPN virus in a population sample with a high incidence of carriers. The largest pool size required fewer cultures and manipulations; therefore, it was more economical and efficient. One hundred culture tubes test 500 fish at 5 fish per pool, but 1500 fish at 15 per pool. The latter aspect is particularly relevant to qualitative tests of production lots, and the data clearly support the use of 10- or 15-sample pools for this purpose. The use of progressively larger pools of material is accompanied by progressively larger errors in estimating the indicence of carriers, and by progressively

greater probability of failing to detect virus among populations with a low incidence of carriers.

Since over 90% of the study population of trout were shown to shed virus at one time or another, this particular lot of fish did not permit us to attain the fourth objective of the study — that of determining whether noncarriers remained noncarriers. That answer must await other work.

ADDENDUM

New research findings at the Eastern Fish Disease Laboratory indicate that Egtved virus, the European pathogen which causes Viral Hemorrhagic Septicemia, is common in kidneys of infected fish but may not always be detected in feces of such fish.

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Canadian Records of the Warty Poacher *Occa verrucosa*, with Notes on the Standardization of Plate Terminology in Agonidae

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GRUCHY, C. G. 1969. Canadian records of the warty poacher *Occa verrucosa*, with notes on the standardization of plate terminology in Agonidae. J. Fish. Res. Bd. Canada 26: 1467–1472.

Recent collections of *Occa verrucosa* provide new records for the species in Canada. Terminology for the ridges of bony plates on the bodies of Agonidae is standardized, and a method for enumerating plates is described and illustrated. Several meristic characters of the northern specimens exceed previously published values for the species.

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INTRODUCTION

THE WARTY POACHER *Occa verrucosa* (Lockington) is known in Canadian waters from a single collection of three specimens. These were taken on the west coast of Vancouver Island in 1945 (Barraclough, 1957; Clemens and Wilby, 1961). Previous to 1945 the known range of the warty poacher was from California to Oregon (Jordan and Evermann, 1898). Schultz (1936) inadvertently presented its range as Oregon to Cold Bay, Alaska; in a previous paper (Schultz and Delacy, 1935) the range was recorded as central California to Oregon. Dryfoos (1961) records two specimens from Shelik of Bay, Alaska.

This paper reports additional Canadian records of *O. verrucosa*. Morphological data on these northern specimens are presented. In the past, some confusion existed in meristic data on poachers as plate terminology and plate-counting techniques were poorly defined. Nomenclature for, and a method of enumerating the plates forming the "bony" ridges on the bodies of poachers are also presented.

Fishes used in this study are catalogued in the ichthyological collection of the National Museum of Natural Sciences, Ottawa, Ont; catalogue numbers for the pertinent collections are given.

METHODS AND MATERIALS

The warty poacher was found in two collections made off Graham Island, British Columbia. One specimen (NMC68-312) was taken by Dr D. B. Quayle on May 4, 1961, over a hard sand bottom in 10 fath of water at 54°07′N, 132°06.7′W. Dr Quayle informs me (personal communication) that the specimen was captured in a rocker-type clam dredge and that the associated flora and fauna included loose kelp, hydroids, nudibranchs, soles, and a sea star. Two specimens of warty poacher (NMC65-331) were taken in Naden Harbour entrance, Graham Island (approximately 54°N, 132°30′W) on August 12, 1965 by D. B. Quayle and party while on the Fisheries

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Research Board of Canada vessel *G. B. Reed*. A third collection (NMC67-343) which included two warty poachers was made by Dr N. A. Powell while on board the *A. P. Knight*, west of Amphitrite Point, Vancouver Island (48°55′N, 125°16′W). These specimens were collected on August 22, 1967 in a Digby (Naturalist) dredge in 12 fath of water over a coarse sand bottom. Other fishes captured in the same haul were *Psettichthys melanostictus*, *Lepidopsetta bilineata*, *Citharichthys stigmaeus*, *Ammodytes hexapterus*, and a rockfish, *Sebastodes* sp.

Before discussing the morphological data on these northern specimens (Table 1), it will be advantageous to define the terminology and counting methods used. The bodies of Agonidae

TABLE 1. Meristic and morphometric data on warty poachers from Canadian Pacific wate[illegible]ata fro

Source	Total length (*mm*)	Sex	No. fin rays					No. plate[illegible]				
			First dorsal	Second dorsal	Anal	Ventral	Pectoral	Dorsolateral	Mid-dorsal	Total dorsal	Ventrolateral	Midventral (see text)
NMC68-312												
Graham Is.	89	♀	VIII	6	11	I,2	14	28	6	34	25	3[illegible]29
NMC67-343 #1	149	♀	IX	9	12	I,2	14	31	5	36	26	1[illegible]30
Graham Is. #2	129	♂	IX	8	11	I,2	13	28	6	34	25	2[illegible]30
NMC65-331 #1	93	♂	VIII	7	11	I,2	14	28	6	34	24	4[illegible]30
Vancouver Is. #2	97	♂	VIII	7	10	I,2	14	27	7	34	25	5[illegible]30
Jordan and Evermann (1898)			VII–IX	7–8	10–12	I,2	14–15		7	35–36		54
Freeman (1951)			VIII–X		10–12		14–15 (pr)			34–37		64

[illegible]Lists "plates," not pores.

are girdled by a series of bony plates whose angles form raised ridges running longitudinally along the body, somewhat like the ridges on most seahorses and pipefishes (Syngnathidae). Unlike the syngnathids, however, the plates do not form "rings" (see Herald, 1959), but interdigitate over most of the body in a mosaic pattern (Fig. 1A). In cross section, the trunk of the body of syngnathids is typically septagonal, in agonids it is octagonal; the peduncle of syngnathids is quadrangular, whereas in poachers it varies from pentagonal to octagonal. While identifying the present material, it became apparent that the series of ridges which begin behind the head and run along the body to the caudal fin should be properly named and defined. Because of the differences in structure, Herald's (1959) terminology for the ridges found on syngnathids is unsuitable for the previously undefined ridges on poachers. After studying specimens from 12 genera of Agonidae, I propose the following names for the ridges in poachers.

In the trunk region the plates form a pair of *dorsolateral* ridges (Fig. 1B), one on either side of the mid-dorsal line, which usually disappear posterior to the second dorsal fin and are replaced by a single median *mid-dorsal* ridge (Fig. 1C). Between each dorsolateral ridge and the

lateral line pores, there is a *supralateral* ridge (Fig. 1B, C) which is continuous on both trunk and peduncle. Ventral to the lateral line there is an *infralateral* ridge (Fig. 1B, C) which is also continuous on both the trunk and peduncle. Between each infralateral ridge and the midventral line of the trunk, there is a *ventrolateral* ridge (Fig. 1B). The paired ventrolateral ridges, like the paired dorsolateral ridges, are typically replaced posterior to the anal fin by a median midventral ridge (Fig. 1C). The situation described above is the typical one, and pertains to most specimens studied. In some specimens, however, the ridges on the peduncle vary. The change from dorsolateral to mid-dorsal and ventrolateral to midventral ridges may occur at varying

ata from Jordan and Evermann (1898) and Freeman (1951) are included for comparison.)

			No. dorsolateral plates					No. ventrolateral plates						
Midventral (see text)	Supralateral	Infralateral	Anterior to first dorsal spine	From last ray of D_1 to first ray of D_2	From membrane of D_1 to first ray of D_2	From last ray of D_2 to first mid-dorsal plate	From membrane of D_2 to first mid-dorsal plate	Anterior to anal ray	From last anal ray to first midventral plate	From anal membrane to first midventral plate	Pores in lateral line	No. left branchiostegal rays	Head length / Orbit length	No. vertebrae (from X-rays)
29	33	35	7	4	1	4	1	9	6	2	38	6	4.5	36
30	35	37	6	3	0	4	2	10	5	2	40	6	5.0	37
30	34	35	7	2	0	3	0	10	5	2	39	6	4.5	35
30	32	34	7	4	0	4	0	10	4	0	38	6	5.0	36
30	32	34	7	4	1	3	0	11	5	1	37	6	4.5	35
			7	4		4–5		10–11 9–10	5	1	36–37 34[a]–40	6	(3.5)	37

distances behind the dorsal and anal fins, respectively. Furthermore, a midventral ridge and a ventrolateral ridge, or both, may not be present on the peduncle (Fig. 1D, E). In unusual cases, a mid-dorsal ridge may not be formed (Fig. 1F) posterior to the second dorsal. Apparently the only ridges consistently present and uniform over the body are the supralateral and infralateral ridges.

A precise definition of counting technique is required for the dorsolateral and mid-dorsal plates and especially for the ventrolateral and midventral plates because of their variability on the peduncle. In enumerating the "total dorsal plates" the number of plates on the left dorsolateral and mid-dorsal ridges are added together. Similarly, the "total ventral plates" is the sum of the number of plates in the left ventrolateral and midventral ridges. In the event that neither ventrolateral nor midventral plates are present on the peduncle, a close estimate may be obtained as follows. Count the median junctures of each two pairs of adjacent infralateral plates (Fig. 1G) where a midventral plate would normally occur and add it to the number of ventrolateral plates on the trunk. A similar procedure may be used to estimate total dorsal plates if necessary.

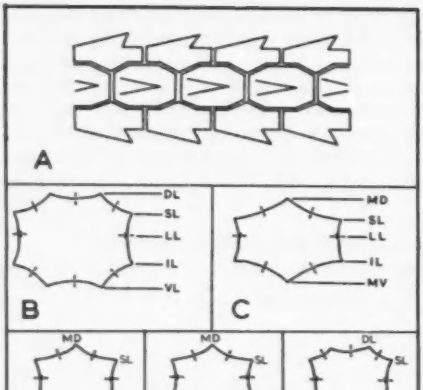

FIG. 1. Schematic representation of several features of Agonidae. A, the interdigitating nature of the plates forming ridges; B, typical cross section through trunk showing ridges formed by plates; C, typical cross section through peduncle showing ridges formed by plates; D, E, F, various combinations of ridges which could be seen on cross sections through peduncle. *Abbreviations in B–F*: DL, dorsolateral; SL, supralateral; LL, lateral line; IL, infralateral; VL, ventrolateral; MD, mid-dorsal; MV, midventral. Short dashes delimit each plate. G, ventral view of part of peduncle; if ventrolateral and midventral plates, or both are absent, enumerate one plate at normal position of midventral plate as shown by hexagon.

The number of supralateral and infralateral plates represent the number of plates in the ridges bearing those names. The plates in these two ridges are uniform in the specimens studied, and are easily enumerated.

There has been some ambiguity in the terminology of the ridges and methods of counting plates in Agonidae in the past. Although specimens from only 12 of the 22 genera of poachers were studied, it is anticipated that the terminology and methods described in this paper will be applicable to all poacher species, and will facilitate future work on Agonidae.

DISCUSSION

The range of the warty poacher extends from California to Alaska, but until the present only five specimens have been recorded north of the state of Washington. It is, therefore, pertinent to describe the meristics of northern specimens. Only one congener, *Occa dodecaedra*, occurs on the Pacific coast of North America, but its range does not extend south of the Alaskan peninsula (Freeman, MS, 1951; Wilimovsky, 1954, 1964). The two species can be readily distinguished by the number of anal rays: *O. verrucosa* has 10–12, whereas *O. dodecaedra* has 14–19.

Previous workers on agonid systematics have used the numbers of total dorsal and ventral plates to advantage, and therefore these data are presented here. However, it is apparent (Table 1), at least in *O. verrucosa*, that the plates of the supralateral and infralateral ridges are consistent and perhaps would be prefreable to "total dorsal" and "total ventral" plates, or both, for systematic work.

With two exceptions, there appear to be no latitudinal trends, nor are there any differences due to sexual dimorphism, in the meristic data in Table 1. The number of plates in each of the supralateral and infralateral ridges is slightly higher in the Graham Island specimens than in those from Vancouver Island. Data are included in Table 1 from Jordan and Evermann (1898) and Freeman (MS, 1951) for comparative purposes. The limits of meristic data described by those authors are exceeded by the present specimens in several instances, viz., number of rays in second dorsal, number of pectoral rays, number of mid-dorsal plates, number of midventral plates, number of supralateral plates between the last ray of the second dorsal and the first mid-dorsal plate, and the number of infralateral plates between the last anal ray and the first midventral plate.

Freeman (MS, 1951) lists the warty poacher as having 34–37 *pairs* of dorsal plates. However, these figures probably include *unpaired* mid-dorsal plates, and under the present terminology, his figures refer to total dorsal plates. Freeman states that there are 34–40 plates in the lateral line, but does not mention the number of lateral line pores. In the specimens of *O. verrucosa* studied, I found that there was always one more lateral line pore than infralateral plates, the additional pore being anterior to the first infralateral plate.

Barraclough (1947) pointed out that the ratio of orbit to head length should be 4.5 and not 3.5 as listed by Jordan and Evermann (1898). The present study agrees with Barraclough and indicates a range of 4.5–5 as a ratio of orbit to head length. Furthermore, Barraclough found there were 0–1 "plates" between the first and second dorsal fins, whereas Jordan and Evermann list 4–5. It can be seen in Table 1 that Barraclough probably counted from the insertion of the membrane of the first dorsal to the first ray of the second dorsal (0–2 dorsolateral plates) but that Jordan and Evermann counted from the last ray of the first dorsal to the first ray of the second dorsal (3–4 (5)) dorsolateral plates.

ACKNOWLEDGMENTS

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Overwinter Survival of Wild Fingerling Brook Trout in Lawrence Creek, Wisconsin

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HUNT, ROBERT L. 1969. Overwinter survival of wild fingerling brook trout in Lawrence Creek, Wisconsin. J. Fish. Res. Bd. Canada 26: 1473–1483.

Overwinter survival of brook trout (*Salvelinus fontinalis*) from the 9-month-old fingerling stage to the 16-month-old yearling stage varied from 35 to 73% during 11 successive winters (1954–65). Mean survival through these first winters of life was 54%.

Survival appeared to be independent of fingerling density most winters, and especially when September densities were less than 2200/km, as they were during 7 of 11 years. Overwinter survival tended to increase with an increase in mean length of fingerling stocks ($r = 0.83^{++}$) and with an increase in winter water temperatures. Intraspecific predation did not appear to be a critical mortality factor. The survival advantage of increased fingerling size was probably related to increased physiological resistance to temperature-associated stresses rather than reduced vulnerability to predation.

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INTRODUCTION

SPORT FISHERIES for wild brook trout (*Salvelinus fontinalis*) are often highly dependent upon yearlings, trout that have survived their first winter of life. In Lawrence Creek such trout normally dominated both the yield and reproduction by the population. For example, during the 1955–57 fishing seasons, yearlings accounted for 50–90% of the seasonal harvests, and during a 14-year period (1953–66) yearlings accounted for an average of 75% of the eggs spawned annually. By contrast, age-0 fingerling trout made no contribution to the sport fishery, even during years when there was no minimum size limit, and no female fingerlings attained sexual maturity in Lawrence Creek (McFadden, 1961; Hunt et al., 1962). However, even though fingerlings made no direct contributions, the numerical strength of these fingerling stocks and the proportions of these stocks that survived their first winter of life were important parameters of the population because the survivors were the yearlings that did constitute the major components of the fishery and spawning stock.

In Lawrence Creek overwinter survival from the 9-month-old fingerling stage to the 16-month-old yearling stage averaged 54% during 11 successive winters (1954–65), but the highest rate of survival (73%) was 2.1 times greater than the lowest rate (35%).

Was this two-fold variation due largely to chance events or was survival intrinsically regulated? If the latter were true, and if regulatory mechanisms could be identified, management efforts could then be directed at ameliorating them, and as a consequence, greater recruitments of yearlings would be realized.

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Of the many factors that might have influenced overwinter survival of fingerling brook trout, these four will be considered: (1) mean length of fingerling stocks in September; (2) numerical density of fingerlings in September; (3) winter water temperatures; and (4) numbers of older brook trout present in September (as potential predators, or competitors, or both).

METHODS

Lawrence Creek normally supports a dense population of wild brook trout averaging approximately 3 trout/m in September. The stream is 5.4 km long from the junction of its two main tributaries to its termination at the Lawrence Flowage. All but 300 m of the lower portion of the stream is included in a public hunting and fishing area. Lawrence Creek has a surface area of 4.8 ha and an average width of approximately 8 m.

Based on knowledge derived from trout population estimates in 1953 and 1954, the Wisconsin Conservation Division selected Lawrence Creek as the site for a long-term, year-round investigation of the management, population dynamics, and ecology of a brook trout population. A research station was established near the stream in the spring of 1955. A compulsory registration-type creel census was also initiated in 1955 and it continued through the 1967 fishing season.

During 1955–58, electrofishing gear was used to make Petersen-type population estimates each April and September. During the 1959–67 period three estimates of the trout population were made annually. Estimated numbers of trout in each 2.5-cm group were usually assigned to age-groups according to the proportions of known-age (finclipped) trout in each grouping. Where data from known-age trout were inadequate, scale samples were used.

Stream temperatures were obtained from two Taylor (Model 1100) thermographs installed in November 1956. Hourly temperatures read from the thermograph records were tallied to derive the monthly mean temperatures referred to in this paper. Monthly summations of degree-hours were obtained from computer summaries. A digital voltmeter was modified to convert and transfer chart readings directly to punch cards (Lovshin, MS, 1966).

Additional details of stream morphometry, the fishery, and research techniques employed at Lawrence Creek have been reported by McFadden (1961), Hunt et al. (1962), and Hunt (1966).

RESULTS

Overwinter Survival in Relation to Fingerling Size

Overwinter survival among 11 fingerling stocks tended to increase with an increase in the average length of these stocks going into the winter (Fig. 1).

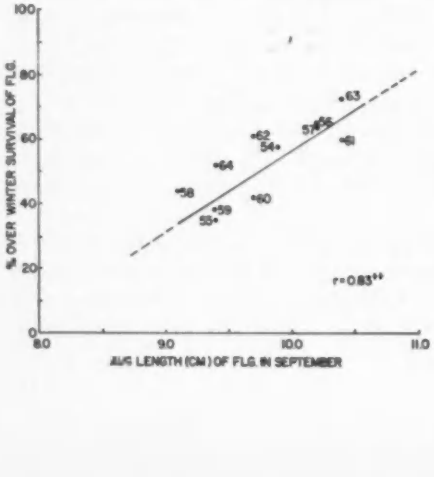

FIG. 1. Overwinter survival rate of fingerling stocks in relation to their average length the previous September.

Seemingly small differences in the average lengths of these stocks in September appeared to have rather large effects upon subsequent overwinter survival. Average lengths of these stocks varied only 14%, whereas overwinter survival rates varied more than 200% (Table 1).

TABLE 1. Number, average total length, and overwinter survival of fingerling (age 0) and adult (age I+) brook trout in Lawrence Creek.

	Fingerlings			Adults		
Sept. of the year	No.	Avg length (*cm*)	% overwinter survival	No.	Avg length (*cm*)	% overwinter survival
1954	13,523	9.9	58	3,045	19.6	54
1955	5,720	9.4	35	3,078	17.5	39
1956	10,853	10.2	65	950	20.3	51
1957	13,258	10.2	64	3,621	19.3	57
1958	4,166	9.1	44	5,028	17.8	54
1959	22,646	9.4	38	1,698	19.3	24
1960	8,507	9.7	42	3,375	18.3	25
1961	14,313	10.4	60	2,624	19.3	47
1962	7,611	9.7	61	4,748	17.8	53
1963	10,367	10.4	73	3,180	18.8	52
1964	9,680	9.4	52	4,951	17.8	43
11-year avg	10,968	9.9	54	3,300	18.8	45

If growth of these fingerling stocks during their first summer of life had been inversely related to their density, the relationship in Fig. 1 could have been caused by an inverse relationship between fingerling density and overwinter survival, i.e., strong fingerling stocks would exhibit both slow growth during their first summer of life and poor survival during their first winter of life. However, first-summer growth was neither inversely dependent or directly dependent on fingerling density (Fig. 2). Within the five-fold range of fingerling densities that existed, growth was best at intermediate densities and

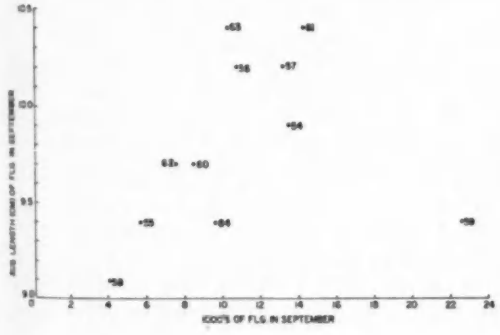

FIG. 2. Average lengths of fingerling stocks in September in relation to the number present in September.

fell off at both low and high densities in a dome-shaped pattern quite different from the direct linear relationship between fingerling size and overwinter survival (Fig. 1).

The remarkably low variability in first-summer growth of brook trout in Lawrence Creek has been previously cited by McFadden et al. (1964) who suggested that perhaps "in some populations numerical adjustments to density and food supply tend to precede adjustments in growth rate and tend to be so effective that growth rate varies but little." My data, which include even greater ranges in numerical density than those encountered by McFadden, certainly support his contention.

Observations of overwinter survival of fingerling stocks after the winter of 1964–65 were not included in the foregoing analyses because of changes in the experimental conditions at Lawrence Creek due to intensive man-made alterations of the trout habitat. However, based on the results of the studies summarized in Fig. 1, a short-term corollary experiment was conducted during the winter of 1967–68. The experiment involved a test of the following hypothesis: If the average lengths of fingerling stocks influence their relative overwinter survival, larger-than-average fingerlings within a cohort should survive their first winter of life better than those that are smaller than average size.

The 1967 year-class numbered approximately 7895 in September 1967. During the first electrofishing run to derive this estimate, 450 fingerlings were measured. Their average length was 9.9 cm. On the second electrofishing run 823 fingerlings, all larger than average size, were marked by clipping the top lobe of the caudal fin. A second lot of 1009 fingerlings, all smaller than average size, was marked by clipping the bottom lobe. The lot of larger fingerlings averaged 10.9 cm and the lot of smaller fingerlings averaged 8.9 cm when marked.

During the first week in April 1968, overwinter survivals of these two lots was determined in conjunction with the routine Petersen population estimate of all trout in the stream. Overwinter survival of the larger fingerlings was 60% whereas survival of the smaller fingerlings was only 52%. Although the difference in survival rates was only 8%, a chi-square test indicated it was a statistically significant difference ($\chi = 9.7^{**}$).

Overwinter Survival in Relation to Fingerling Density

The number of fingerlings in September ranged from 770 to 4200/km during 1954–64. Mortality during the winter reduced these stocks to densities of 340–1600 yearlings/km in April. Densities of fingerling stocks in September and yearling stocks in April varied by factors of 5.4 and 4.7 respectively, yet overwinter survival rates varied by a factor of only 2.1.

Among all 11 fingerling stocks, overwinter survival did not appear to be density-dependent and especially among the seven stocks numbering less than 2200/km in September (Fig. 3). During most winters, differences in body size probably influenced survival more than stock densities. However,

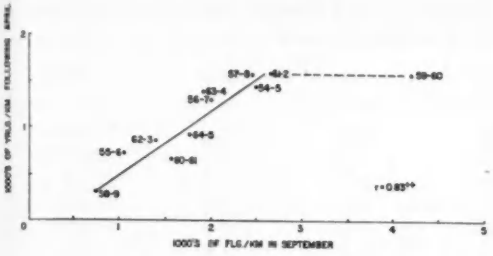

FIG. 3. Density of yearling brook trout in April in relation to the density of fingerlings present the previous September.

the four stocks of fingerlings having densities of 2500–4200/km, including the exceptionally strong 1959 year-class, were all reduced to about the same density of April yearlings. Among these four stocks compensatory mortality may also have been an important factor influencing the number of yearlings recruited to the fishery.

The greatest number of April yearlings (1600/km) was derived from the 1961 stock of fingerlings, not the exceptionally strong 1959 year-class. The 1959 year-class was 60% stronger than the 1961 year-class at 9 months of age, but the average length of the 1959 year-class was 11% less. As the data in Fig. 1 suggest, such a seemingly small difference in average size could have contributed to the much lower overwinter survival of the 1959 year-class (38%) in comparison with the 1961 year-class (60%) in addition to any density effects on their relative survival.

Overwinter Survival in Relation to Stream Temperature

Water temperature of Lawrence Creek normally ranged from 0 C recorded 5–10 days annually to 24 C recorded 1–3 days annually. Weekly means ranged from 1.7 to 18.3 C during 1956–65. During the months of November through March, monthly means were lowest in January during four winters, lowest in December during two winters, and lowest in February one winter. During the other two winters, January and February means were similarly low. Nine monthly means for December, January, and February averaged 4.6, 4.0, and 4.7 C respectively. Nine monthly means for November and March, the months bracketing the 3 coldest months, both averaged 7.1 C (Table 2).

Reimers (1963) observed that feeding activity and movement of stocked rainbow trout (*Salmo gairdneri*) in Convict Creek increased noticeably whenever stream temperatures rose above 4.5 C. He also found that weekly natural mortalities of these stocked trout were associated with periods of poor body condition and oscillations of stream temperatures above and below the 4.5 C threshold during the critical late winter period. Deaths were attributed to temperature-induced catabolism.

The percentage of hours in which the temperature of Lawrence Creek exceeded 4.5 C monthly during December through March of 1960–65 are illustrated in Fig. 4. If these hourly summations are typical for Lawrence Creek, temperature-associated stresses should be greatest in January most

TABLE 2. Monthly mean water temperatures (C) of Lawrence Creek during nine winters.

Winter of	Nov.	Dec.	Jan.	Feb.	Mar.
1956–57	[a]	[a]	4.3	4.4	7.5
1957–58	6.9	4.9	5.0	4.7	8.2
1958–59	7.4	4.5	3.4	4.6	7.5
1959–60	6.6	6.7	3.7	4.6	5.7
1960–61	5.4	3.0	3.1	5.8	7.2
1961–62	7.2	4.5	4.0	3.9	7.4
1962–63	7.4	5.5	4.6	4.7	7.6
1963–64	8.0	3.3	4.8	5.3	7.0
1964–65	7.8	4.8	3.8	4.7	6.2
Nine-winter avg	7.1	4.6	4.0	4.7	7.1

[a]No data collected until January 1, 1957.

winters. December and February may also be critical some winters, but by March stream temperatures are normally much improved. During the five winters for which temperature summation data are available, the hours of temperature above 4.5 C per month averaged 49% for December, 34% for January, 51% for February, and 72% for March (Table 3).

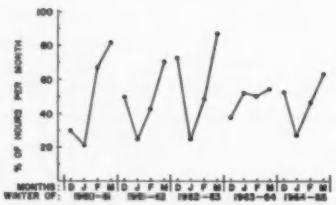

FIG. 4. Percentages of hours in which the temperature of Lawrence Creek exceeded 4.5 C during the December–March periods of 1960–65.

In Fig. 5 overwinter survivals of five fingerling stocks are plotted against hourly summations of stream temperatures above 4.5 C during December, January, February (Fig. 5A), and during January only (Fig. 5B). Both diagrams suggest a direct relationship between overwinter survival and temperature. It is possible that these survival patterns are not really related to temperature but are simply artifacts produced by the relationship between fingerling size and survival (Fig. 1). However, such does not seem to be the case. The 1961 and 1963 fingerling stocks both averaged 10.4 cm in September, but the 1963 stock survived better during the more moderate winter. Similarly, the 1962 and 1960 stocks both averaged 9.7 cm and their numerical densities were similar, but the 1962 stock had the higher survival during the more moderate winter.

TABLE 3. (A) Number of hours of water temperature above 4.5 C during 4 winter months.

Winter of	Dec.	Jan.	Feb.	Mar.	Sum
1960–61	220	155	447	611	1433
1961–62	370	262	292	530	1454
1962–63	542	263	329	645	1779
1963–64	286	394	358	411	1449
1964–65	393	202	317	477	1389
5-winter avg	362	255	349	535	1507

(B) Per cent of the total hours per month during which the water temperature was above 4.5 C during 4 winter months.

1960–61	30	21	67	82	49
1961–62	50	35	43	71	50
1962–63	73	35	49	87	74
1963–64	38	53	51	55	49
1964–65	53	27	47	64	48
5-winter avg	49	34	51	72	54

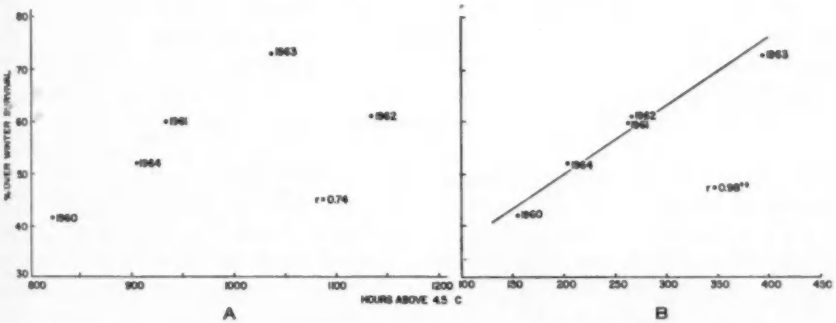

FIG. 5. Overwinter survival rates of fingerling stocks in relation to the hours of water temperature above 4.5 C during December–February periods (A) and during January only (B) of 1960–65.

DISCUSSION

Although size-related survival has seldom been quantitatively measured in wild fish populations, tacit recognition of its validity underlies the gradual changeover in trout stocking policies. The practice of planting fertilized eggs or fry was gradually replaced by stocking fingerlings which was, in turn, largely replaced by stocking of catchable or legal-size trout (Brynildson et al., 1966; Cooper, 1959). My data suggest that there may be even greater sensitivity between size and survival than most fish culturists have heretofore recognized.

Quantitative examples of size-related survival in wild salmonid populations are described by Foerster (1954), Johnson (1965), and Ruggles (1965). Foerster reported that an increase in average size of seaward migrating sockeye salmon (*Oncorhynchus nerka*) smolts from 4 to 10 g was associated with a three-fold increase in the rate of return of adult spawners. Johnson summarized and supplemented earlier data from Ricker (1962) to demonstrate a similar direct relationship between average size of sockeye smolts and subsequent oceanic survival. Ruggles demonstrated a direct relationship between growth and summer survival of juvenile sockeye salmon in Owikeno Lake prior to emigration. He also observed that summer survival was inversely related to stock density. Johnson (1965) also stated that "predation is believed to be the critical mortality factor in all the life history stages of sockeye after their emergence from the spawning grounds as fry."

In Lawrence Creek older brook trout were the only fish numerous enough to constitute potentially serious predators of fingerlings during the winter. However, two sources of evidence indicate that intraspecific predation was probably not a critical determinant of fingerling survival through the winter months. In the larger three-dimensional schematic illustrated in Fig. 6, overwinter survival rates of four pairs of fingerling stocks of similar densities are

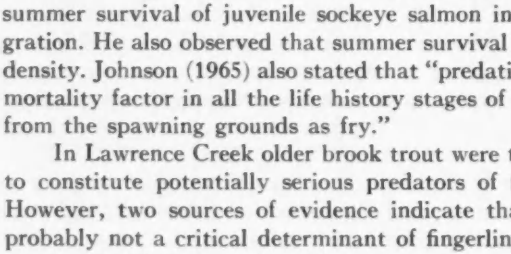

FIG. 6. Overwinter survival rates of fingerling stocks in relation to their density and the density of coexisting stocks of older trout the previous September.

compared in relation to different densities of adult trout (potential predators). The height of each pin represents an overwinter survival rate. The position of each pin is at the appropriate intersection of fingerling density and the contemporary density of older trout. The smaller schematic indicates the theoretical relationship that should exist if intraspecific predation was a major determinant of fingerling survival through the winter. However, the larger empirically based schematic suggests such a relationship did not exist. Among pairs of fingerling stocks of approximately similar density, survival was not higher for the stock coexisting with the lower density of older trout.

Intraspecific predation as a major source of fingerling mortality is also refuted by examination of nearly 1500 trout stomachs collected during 1960–66. Only 11 fish, 7 of which are mottled sculpins (*Cottus bairdi*), were found. No trout fry or fingerlings were found even through stomachs from older trout were collected every month during 2 years. During the first 3 months after emergence of the 1963 year-class, an average consumption of 15 fry/adult trout per day would have accounted for only 10% of the estimated mortality of fry. However, no fry were found in a sample of 30 adult stomachs (10 stomachs/month) collected during that period, nor were trout fry ever found in stomachs of adults collected during other periods of fry emergence. One such sample included 100 adult stomachs collected in March from one of the areas of heaviest spawning. If intraspecific predation was not significant at the fry stage, as seemed to be the case in Lawrence Creek, it should have been even less so at the fingerling stage if increased body size of the prey was critical.

Other potential predators of trout observed at Lawrence Creek included kingfishers and great blue herons, which are not resident during some winter months, water snakes and snapping turtles, which are not active during the winter, and mink and raccoons, which are active year-round. During two April electrofishing inventories several dozen live trout were collected that bore multiple slashlike wounds. These wounds could not have been caused by birds, but were most probably inflicted by raccoons. Although the extent of fingerling mortality caused by any of the predators listed is not known, it seems unlikely that such predation would be influenced by minor variations in fingerling size from winter to winter. Thus, the available evidence indicated that the survival advantage of increased size was not due to a reduction in predation.

There was evidence, however, that absolute size could have influenced overwinter survival by modifying thresholds at which physiological stresses were either fatal or directly contributory to other causes of natural mortality. Growth data, collected monthly during three winters, indicated that fingerlings were not able to maintain their body weight proportional to their length (Fig. 7).

Condition factors (R) declined to their lowest values (1.38–1.50) in December and had only improved slightly in January during two of the three

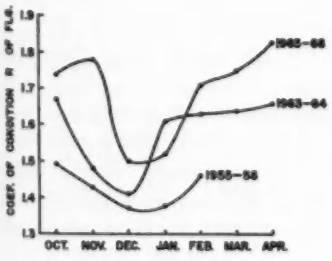

FIG. 7. Coefficients of condition (R) of three fingerling stocks during the winter months.

winters of sampling. Some male fingerlings (approximately 5%) mature sexually but no female fingerlings spawn. Consequently, declining condition factors must imply physiological demands upon energy reserves stored in body fat in lieu of adequate food consumption or digestion rather than explusion of reproductive products. A chemical analysis of a sample of fingerlings collected in January 1963 also revealed that fat comprised less than 1% of their body weight. This compares with a more healthy fat content of 3% for a sample collected 3 months later. It seems reasonable to conclude that such physiological deterioration would be more adverse for small fingerlings than for large ones (Lindroth, 1965).

Cooper (1953) reported that the coefficients of condition (R) of wild brook trout (age 0 and I) in three Michigan streams also reached their lowest values during the winter. Lowest condition values occurred in February in two streams and in January in the other stream. Resumption of growth and recovery from periods of low coefficient of condition began at least a month or two later in the Michigan streams than in Lawrence Creek.

Reimers (1963) concluded that overwinter survival of the domestic stocks of rainbow trout planted in Convict Creek was largely a matter of endurance dependent upon their fat reserves as they entered the winter period of inadequate nutrition. Among the various lots of domestic trout that he stocked, overwinter survival was twice as high (38%) for those raised on fresh or fresh-frozen animal diets as for those raised on pelleted dry diets only. Although the combination of declining vigor and the necessity to compete with wild trout for safe shelter may have contributed to the high winter mortality among the domestic stocks, mortality due to predation or large-scale losses due to severe ice or snow conditions did not appear to be critical in Convict Creek.

The average overwinter survival for 23 lots of the catchable-size trout stocked in Convict Creek was only 27%, or well below the 54% average for fingerling brook trout in Lawrence Creek. Higher survival of brook trout in Lawrence Creek undoubtedly reflects the inherently greater vitality of wild trout versus hatchery-reared trout and Lawrence Creek is also considerably warmer during the winter than Convict Creek. For example, during the months of December through March, temperatures above 4.5 C were recorded 54% of the hours for Lawrence Creek (five-winter average) but only 16% of the hours for Convict Creek (one winter only). Anchor ice has never been observed in Lawrence Creek and much of its surface remains unfrozen throughout the winter.

In summary, the observed rates of survival of brook trout in Lawrence Creek from the September fingerling to April yearling stage were probably closely related to their absolute size in September. Overwinter survival did not seem to be density-dependent when fingerling stocks numbered less than 2200/km in September, as they did during 7 of 11 years, and density was clearly critical for only one of the 11 fingerling stocks, the exceptionally strong 1959 year-class. This was the year-class that was 60% stronger at 9 months of age than any of the other 10 year-classes. The inherent survival value of

increased body size was probably related to increased resistance to temperature-induced physiological stress rather than reduced vulnerability to predation or intraspecific competition. Highest overwinter survivals (1956, 1957, and 1963 stocks) were associated with the combination of large fingerlings of intermediate numerical density and relatively mild winters.

If the inferences of this study are valid, sport fisheries sustained by wild brook trout populations like the one in Lawrence Creek should benefit from management practices which improve first-summer growth of brook trout or moderate stream temperatures during the winter. Improvements in either or both parameters will tend to increase the numbers of yearlings recruited to the fishery.

ACKNOWLEDGMENTS

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Population and Production Ecology of Zooplankton in Ogac Lake, a Landlocked Fiord on Baffin Island[1]

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Collections were analysed from the three basins of the lake in 1957, and from the middle basin of the lake and a fertilized polyethylene column in 1962. The abundant copepod, *Pseudocalanus minutus*, was basically annual in life cycle, spawning a number of almost synchronous broods (egg sacs) in the short period of abundant food supply in early summer. The number of young per brood was dependent on size of females, and the number of broods was independent of the amount of food during the reproductive season. The species was concentrated in rich food supply at the halocline and at depth. There was no diurnal vertical migration in summer, but ontogenetic descent of older stages appeared adapted to "seeking" colder water. The species is much smaller in the lake than in the nearby sea, and this, as well as seasonal size changes, can be attributed to temperature effects. Females, but not males, roughly doubled weight ("Brooks' Law") between stages in constant conditions. Maximum development rate was about 0.4 stages/day at 6–7 C, similar to laboratory estimates reported for temperate populations. Growth is not isometric; *P. minutus* grows stouter as it grows longer. Net production (some 30% as eggs) ranged from 410 to 510 mg C/m² per year in various basins and years, and was less than doubled in the fertilization xperiment.

The copepod *Oithona similis* was strictly annual and produced almost synchronous broods (two egg sacs), which were successfully recruited only in late summer, on different food requirements from those of *P. minutus*. It was nonmigratory in summer, and its vertical distribution, like its size, was little influenced by temperature. Weight increments were only about 50% between copepodite stages, and development between egg and adult took at least 1.2–1.6 months. Production ranged from 202 to 347 mg C/m² per year and was not increased in the fertilization experiment.

The chaetognath *Sagitta elegans* was annual in the lake, reaching full size but suspending development during summer. Much reproduction occurred before and after the short period of successful recruitment of young, and size of new generation was proportional to the number of adults but not the abundance of food for the young present during this period. Overwinter mortality was less in the shallow outer basin than in the middle and inner basins, where *S. elegans* lived below their food species. Ontogenetic ascent of young was followed by descent of older individuals, but immatures showed marked migration into the warm, food-rich halocline at night. The species was much smaller in the lake than in the nearby sea, where it is biennial. In another landlocked fiord, temperatures intermediate between those of Ogac Lake and the nearby sea thwarted a successful annual or biennial cycle by promoting maturation at an inappropriate time of year. Net production ranged from 49 to 318 mg C/m² per year; the wide range is attributable to variable numbers of spawning adults at time of recruitment.

The medusa *Aglantha digitale* had two generations per year in the lake. Successful reproduction may have depended on abundant small particles (phytoplankton) as food for the young, but control of recruitment and subsequent survival remains obscure. Its

[1]The fourth in a series of studies of Ogac Lake.

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scarcity in the outer basin may have been related to forced coexistence with *S. elegans*. *Aglantha digitale* generally occupied mid-depths in the water column, sinking slightly at night, its vertical distribution being little related to temperature. The species grew about four times as long in the sea outside, but the same relationship prevailed between gonad and body size. Production ranged widely between basins and years from 13 to 263 mg C/m² per year, and was not increased by the fertilization experiment.

Other holoplanktonic species in the lake are treated briefly. Of these, the ctenophores (*Beroe* sp.) may have been of some importance in production, and the copepod *Eurytemora americana* was opportunistically abundant and productive in the halocline in 1962. Others, including microzooplankton, added little production.

Among the planktonic larvae of benthos, bivalve (mostly *Mya truncata*?) larvae spent a year in the plankton, as did some polychaetes. These larvae showed marked vertical migrations, especially the older ones. The larvae only achieved an estimated 13% of the production shown by *P. minutus* and *O. similis* combined.

Allochthonous zooplankters brought in by the tides seemed ill-adapted to the lake. The few surviving allochthonous *P. minutus* became smaller in the warm waters, and may have insured gene flow between the lake and the sea. The allochthonous zooplankton were important as organic enrichment, equivalent to about one-half the annual autochthonous zooplankton production.

Some general conclusions follow. Niche diversification is clear in the lake, and some widespread arctic species may be excluded competitively. The marked seasonality of the lake (and other waters of middle and high latitudes) means that controls of population size and growth occur when food is in excess. The studies of vertical distribution and migration demonstrate the necessity for close vertical spacing of samples, and detailed consideration of different stages and size classes. Support is partial at best for the theory that vertical migration is adapted to control growth and development and maximize rates of increase in thermally stratified waters. The results nevertheless stress the over-riding influence of temperature on body size of zooplankters. Overall zooplankton production was about 1 g C/m² per year. "Herbivore" production was about 7% of primary production in 1962, and was little enhanced by a seven-fold increase of primary production in the fertilization experiment. Predator production ranged between 16 and 68% of "herbivore" production. Production/biomass ratios averaged about 3:1, but wide variations occurred, such that the ratios cannot be considered to be "physiological" or determinate for a species or a system. It is argued that production cannot be measured or "explained" in highly seasonal environments like Ogac Lake without detailed quantitative studies of life histories.

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INTRODUCTION

THE GENERAL CHARACTER of Ogac Lake and its biota have been outlined in the introductory paper to the series of which the present paper is a part (McLaren, 1967a). This landlocked fiord has several features which make it an ideal "natural laboratory" for the study of marine zooplankton. It is replenished by tidal sea water only during one period each month in summer, which makes for a degree of isolation of its zooplankton from advective changes. The fact that it is anoxic below certain depths means that the entire plankton-inhabited water columns can be sampled more easily. It has three semi-isolated basins, which afford interesting comparisons. Its salinity is not much lower than that of arctic surface waters in general, so that the dominant zooplankters are not brackish-water specialists, but species that are widespread and abundant in the waters outside the lake. On the other hand, the warm temperatures in

the lake are not experienced by these species in their normal arctic environments; to this extent, the effects of temperature can be studied independently of other aspects of high latitudes. Finally, in common with other arctic zooplankton populations, those of Ogac Lake develop and grow slowly and relatively synchronously, which facilitates quantitative studies.

When I began field studies at Ogac Lake, the ideas of trophic ecology were becoming prominent; the assessment of energy flow through organisms and ecosystems was being promoted almost as an end in itself, although descriptive and predictive generalizations and models were being sought by some. It was my initial intention to make a complete assessment of zooplankton production in the lake. This ambition will have to await studies of respiration and other aspects of the production system. Nevertheless, this paper apparently contains the first attempt at a complete assessment of net production of all zooplankton species in a marine or freshwater habitat. Meanwhile, my bias has changed; one major intention of this study is to show that the control of zooplankton production cannot be understood without studies of life cycles, population dynamics, and adaptive strategies of the producing organisms.

Few zooplankton species, marine or freshwater, have been studied in the quantitative detail presented in this monograph. Many details may appear unnecessary to some readers. To these I plead that some general conclusions in the Discussion depend on just such details.

MATERIALS AND GENERAL METHODS

Seasonal Sampling Methods in the Field

The core of the material in this monograph is based on a series of vertical net hauls taken at roughly biweekly intervals from June to October in 1957 and June to August in 1962. The dates of sampling are given in tables and figures. All hauls were made near the centers of the three lake basins, usually within a few meters of one another on any sampling date. To catch very small forms, nets with no. 20 mesh (apertures, 76 μ) were used except in late September 1957, when sample bottles were in short supply. Such fine-mesh nets have low and perhaps variable efficiency because of clogging, and may be avoided by larger zooplankters. Therefore, single hauls (or two combined) were made with nets of no. 6 mesh (239 μ). Except for the first series in June 1957, the no. 6 nets were hauled vertically at ca. 0.5 m/sec from the anoxic depths which began at about 20 m in the outer basin and 30 m in the middle and inner basins of the lake, so that the entire inhabited water columns were sampled. For reasons that are unjustifiable in retrospect, in 1957 the no. 20 nets were usually hauled (two hauls combined) from 20 m to the surface. Fortunately, as will be evident in the descriptions of vertical distributions of several species in the text, young and small individuals, whose numbers were estimated by these nets, were almost all found above 20 m. All vertical hauls of the seasonal series in 1962 were from the anoxic depths.

Both the no. 6 and no. 20 nets used in 1957 were 30 cm in diameter and of the ordinary conical form. The no. 6 nets were designed for use elsewhere, and had canvas midsections for constriction by closing devices. This lowered their filtering efficiency (see below).

In 1962, a Clarke–Bumpus sampler, removed from its frame, was used to make two to four combined vertical hauls on each date. No back-revolutions on the flow meter were observable in the clear water when the sampler was lowered sufficiently slowly. The sampler was fitted with a no. 20 net on the first three sampling dates and thereafter with a no. 6 net. A 30-cm no. 20 net was used to make one parallel haul on each later date. To sample large forms in 1962, a haul was made on each date with a net of no. 6 mesh, 0.5 m in diameter; the large net was used a day later than the small nets on one occasion on June 23.

Great care was taken in the field to wash down the contents of nets and otherwise assure preservation of the entire contents of a haul. Hauls in summer were made on calm days, to ensure that they were vertical. Samples were discarded and hauls repeated when any doubts were entertained about their adequacy. The hauls were made in the deepest parts of basins, but were not rigorously positioned.

Laboratory Sampling of Seasonal Series

About 85 samples were analyzed in detail to follow seasonal changes. Some of these involved many days of laboratory work. The intention of the laboratory sampling was to estimate numbers and often sizes of every stage of every species in the zooplankton.

The coarse-net samples were first searched under a dissecting microscope for larger animals, mainly medusae and chaetognaths, all of which were counted, measured, and removed. Then thoroughly mixed subsamples were taken by large-bore suction pipets and volumes determined in small graduated cylinders. The sizes of subsamples were chosen according to the abundance of the organisms. Complete counts were made in these subsamples of stage IV–VI copepodites of the abundant copepod *Pseudocalanus minutus* from 1957, and of the adult females (VI ♀) from 1962.

The large organisms were first removed from the fine-net samples and then subsamples were taken as above. Sometimes the subsamples themselves were further diluted and subsampled in the same way for particularly abundant stages of species. Under the dissecting microscope the intermediate sized animals (e.g., copepodite stages of *P. minutus*) were identified, counted, measured, and removed. Smaller ones (bivalve larvae, copepodites of *Oithona similis*, small larvae) were counted, or measured, or both, but were left in the subsamples along with the residue of nauplii, eggs, Protozoa, phytoplankton, etc.). The subsamples were then concentrated by settling in small vials. Arbitrarily sized, well-mixed fractions of these concentrates were removed by eyedroppers and placed on covered slides for counts and measurements under higher magnification of the compound microscope. Complete counts of such zooplankton fractions were made to eliminate sampling errors of partial or field counts. These arbitrary fractions were related to the larger subsamples through counts of the same species (usually copepodites of *O. similis*) in both the fractions and the subsamples. Such counts in the small fractions ranged from 41 to 209, and in the subsamples from 107 to 1198, so the transformations, assuming randomness, are probably reliable.

The intention of the above subsampling practises was to allow conversion of counts between fine-mesh and coarse-mesh samples. It was found by χ^2 tests of sample counts that although copepodite stages IV, V, and VI (adult) of *P. minutus* were sometimes sampled differently by the coarse and fine nets on a given date, there was no overall bias to suggest that the stage IV animals (about 0.3 mm cephalothorax width) were consistently retained less than stage V or VI by the coarse net. Stage III was slightly undersampled, and stages II and I consistently so, by the coarse net. Therefore, stages IV–VI were used for conversions of counts between the two nets for 1957, and stage VI for 1962. Of 24 such conversions from 1957, 11 were based on counts from both nets of more than 100, 12 on counts of over 50 (the whole samples) from the fine and over 100 from the coarse net, and 1 involved the entire fine-net sample of 32 individuals. In 1962, the coarse-net counts ranged from 169 to 401, and the fine-net counts from 81 to 145.

Conversion of Seasonal Samples to Quantitative Estimates

All abundances in the seasonal series are expressed in numbers per m^3 in this paper. In 1957, the standards for quantitative estimates were the samples collected by the deep vertical hauls taken at 0.5 m/sec with the no. 6, 30-cm nets. Since these nets were equipped with a canvas midsection, they could not be assumed to be 100% efficient, although other conical, coarse-mesh nets may be so. A similar net was calibrated from the M/V *Calanus* in southern Hudson Bay in September 1960. To do this, the net was mounted on a frame adjacent to a Clarke–Bumpus sampler, modified and open for vertical towing, and fitted with the same mesh. The whole unit was lowered slowly, so that no back-revolutions of the flow meter were apparent in the first few meters of lowering, and then raised from 50 m. Seven paired samples were taken altogether, at

different speeds. Subsamples of larger copepods (*Calanus* spp. copepodites and stage IV–VI copepodites of *P. minutus*) allowed estimation of filtering efficiency (i.e., independently of mouth area) of the 30-cm net against the calibrated Clarke–Bumpus sampler. These efficiencies were 0.64, 0.82, 0.73, 0.52, 0.61, 0.43, and 0.39 at towing speeds of 0.31, 0.37, 0.40, 0.48, 0.57, 0.57, and 0.73 m/sec respectively. Efficiency was inversely and apparently roughly linearly related to towing speed, not following the curvilinear function expected for more simple nets (Kobayashi and Igarashi, 1956). The efficiency of sampling at 0.5 m/sec is calculated from the linear regression as about 0.60, and the 95% fiducial limits of this estimate are about ±0.10. Although these limits are rather wide for an estimate of average efficiency, all quantitative estimates in numbers per m^3 in 1957 are based on the assumption that the standard coarse-mesh net was 60% efficient in vertical tows.

Estimates for 1962 are based on the Clarke–Bumpus samples. The sampler was calibrated without a net by being towed vertically from known depths at 0.5 m/sec. It filtered 4.53 liters/revolution, assuming 100% efficiency.

Reliability of Estimates in Seasonal Series

A series of samples from 1962 can be compared to give some impression of the combined sampling errors involved in field and laboratory (Table 1). Here counts of copepods from the known volumes filtered by the Clarke–Bumpus sampler are compared with counts from estimated

Table 1. Comparison of adult ♀ *P. minutus* in samples taken by two to four combined vertical hauls of the Clarke–Bumpus sampler and by a single haul with a 0.5-m no. 6-mesh net in areas near the deepest part of the middle basin as part of the seasonal series in 1962 (see text).

	Clarke–Bumpus sampler		0.5-m no. 6-mesh net		
Date	No. copepods in sample	No. liters filtered	No. copepods in sample	Estimated no. liters filtered	Efficiency relative to C.–B. sampler
June 8	100	389	349	1382	0.97
22–23	134	544	320	968	1.34*
29	145	514	187	614	1.08
July 8	331	648	177	379	0.91
22	223	389	266	358	1.29*
Aug. 10	401	584	245	502	.71*
22	335	757	169	372	1.03

*Significant difference between numbers per liter.

volumes sampled by the 0.5-m net, hauled from the same depths, in the same general area. The latter volumes are based on the assumption that the net (which had no canvas midsection) was 100% efficient, corrected for the size of subsample in which counts were made. The population densities implied by the two nets were not significantly different (χ^2 tests against theoretical numbers assuming same densities in each pair) in four of seven paired comparisons, and the maximum deviation in relative efficiency was only 34%. Thus the reliability of individual net samples appears to be quite high.

Table 1 indicates another interesting property of Ogac Lake that deserves comment. Each of the paired vertical hauls in Table 1 were made meters and often tens of meters apart, and those of June 22–23 were taken on separate days. Yet the differences in copepod density are rather slight. Gross statistical overdispersion is evident in almost all paired samples taken from

lakes or the sea (see review by Cassie, 1962). The samples from Ogac Lake may reflect the lack of hydrographic sources of grouping in this highly stratified system (see Sutcliffe et al., 1963).

Another source of error may have arisen from differences in sampling stations on successive dates. Abundance of some species in the lake was related to distances from shore. This problem will be discussed in the text in terms of the chaetognath *Sagitta elegans*, the copepod *Eurytemora americana*, and various benthonic larvae. It is probable that some differences between successive sampling dates resulted from imprecise locating of the sampling stations near the deeper parts of the basins.

Fertilized Column Experiments

In 1962, large polyethylene columns (Goldman, 1962), 30.5 m long and ca. 1 m wide, were anchored and suspended in the middle basin of the lake between the anoxic depths and the fresh surface layer. The columns were lowered quickly through holes in the ice, thus trapping populations of zooplankton. Two columns were fertilized identically, and two acted as controls. Details of the experimental methods and effects on plant production are given by McLaren (1969). It is sufficient here to state that by increasing nitrate levels roughly five-fold, large phytoplankton populations were promoted in the two fertilized columns.

The four columns were put down and two were fertilized on June 20. One of these fertilized columns was sampled for zooplankton on June 22, 29, and July 3. This column sank accidentally in early July, and the series was concluded by samples from the other identically fertilized column on July 14, 22, and August 9. The series consisted on each date of two to five hauls of the Clarke–Bumpus sampler, fitted with a no. 6 net and modified for vertical towing, and one to three hauls with a small, no. 20 net, 12.5 cm in diameter. The laboratory methods were the same as those described above for seasonal series from the lake proper.

To distinguish between effects of fertilization and effects of the columns and sampling techniques, samples were compared from the fertilized column on August 9, the unfertilized control column on August 11, and the middle basin on August 10 .The results for the four most abundant species in the lake (Fig. 1) indicate that the small nets used within the columns were adequate for the two copepods, *P. minutus* and *O. similis*. There was perhaps a slight tendency for the medusa *Aglantha digitale* to be underestimated by the small nets (Clarke–Bumpus sampler with no. 6 net) in the columns, as indicated by the comparisons of samples taken by the small net and the large, 0.5-m net in the open basin. The small net of the Clarke–Bumpus sampler was clearly inadequate for the larger specimens of *S. elegans*. In conclusion, the series of samples probably adequately reflected real differences in populations between the fertilized column and the lake, except for the chaetognath *S. elegans*, which was the largest and perhaps fastest swimming member of the zooplankton.

Sampling for Vertical Distributions

Vertical hauls with the Clarke–Bumpus sampler fitted with a no. 6 net and with a small no. 20 net were made around midday through holes in the wasting ice in the middle basin on July 8, 1962. These were made from 27, 20, 15, 10, and 5 m to the surface. The upper 2 m were essentially fresh water, and assumed to be devoid of plankton. The samples were analyzed as for the seasonal series (above), and numbers of species or stages in each depth interval of 20–27, 15–20, 10–15, 5–10, and 2–5 m were calculated by successive subtractions.

Series of horizontal hauls with Clarke–Bumpus samplers were made in August of 1957 and 1962. The lines on which the samplers were towed at 1–2 mph were kept almost vertical by use of very heavy weights, and angles were taken to make the small depth corrections required. The samplers were opened, towed, and closed at depths that probably varied much less than a meter around the mean depth of tow. The amount of water filtered by each tow varied from 0.48 to 1.45 m^3. One series was carried out between about 1030 and 1300 hr on August 21, 1957. Another was taken from about 1115 to 1400 hr on August 13, 1962. The third was carried out at night, between about 2300 hr on August 14 and 0115 on August 15, 1962. A net of no. 10 mesh was used in 1957, and no. 20 in 1962. The depths sampled will be evident on text figures. The samples were analyzed in the laboratory according to the procedures outlined above; often whole samples were counted.

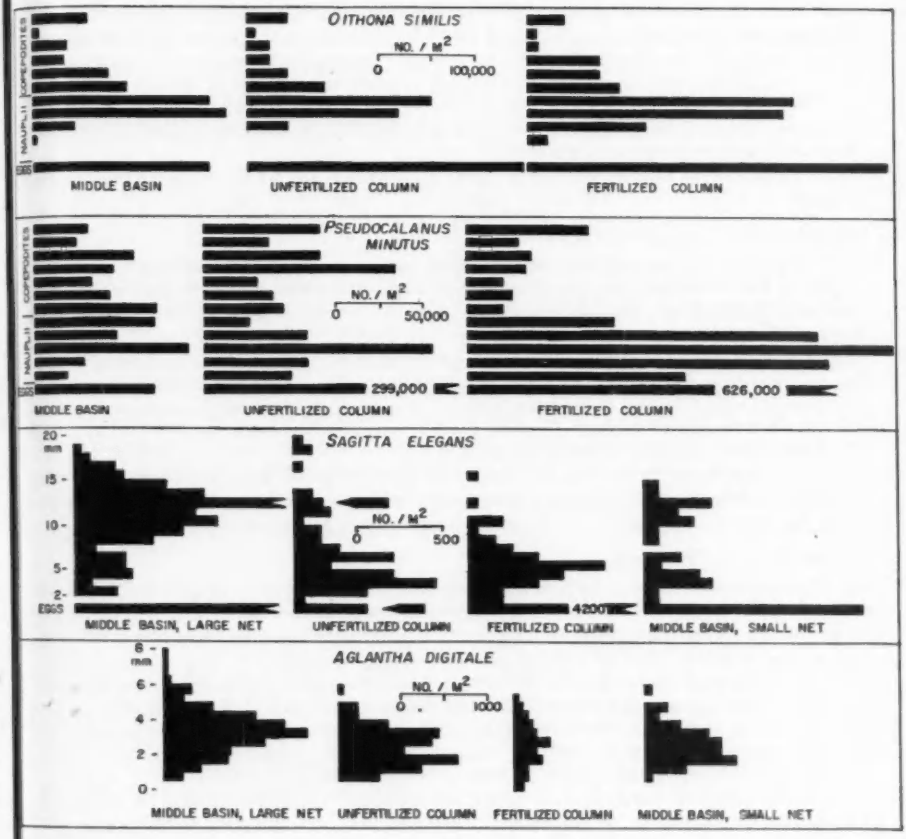


FIG. 1. Comparisons of estimates of abundance of four species of zooplankton in the middle basin of Ogac Lake and in polyethylene columns suspended in the lake; estimates based on large and small nets as shown (see text).

SPECIAL PLANKTON SAMPLES

In addition to the regular seasonal series and samples to study vertical distributions, plankton samples were taken for a variety of special purposes.

The plankton of the inflowing tide was sampled once or twice during each series of tidal inflows in 1957 and 1962. On each occasion in 1957, a 0.5-m net with a no. 0 mesh and a flow meter mounted centrally in its mouth, was held in the inflow current near the height of the tide. This net was assumed to retain everything as large as or larger than stage IV copepodites of the copepod *Calanus glacialis*, which was usually abundant. A simultaneous sample was taken with a 30-cm, no. 6 mesh net. This net was assumed to capture smaller forms as well as older copepodites and adults of *C. glacialis* with the same efficiency, and could thus be qualified from the metered net. Unfortunately, no finer mesh nets were used in 1957. In 1962, a Clarke–Bumpus sampler with an no. 6 net was used to quantify simultaneous samples in the inflow with a large no. 0 and a small no. 20 net.

Series of vertical hauls with a no. 0, 0.5-m net were taken through natural holes and fissures in the ice in June and early July of 1962. The primary purpose was to study distribution of cod eggs and larvae (Patriquin, 1968), but the nets also captured samples of *S. elegans*, which will be considered here. Dates and distributions of these samples will be evident in the text.

Plankton samples were taken just off the bottom in shallow water near and within the halocline in June and early July of 1962. These were secured by Clarke–Bumpus samplers, equipped with no. 6 nets, propelled by scuba divers.

Precise depths were maintained by use of depth gauges and by observing contours on the bottom.

Weights and Carbon Determinations

Dry weights of copepods were determined by a balance accurate to 5 μg. Formalin-preserved copepods were measured in length, rinsed quickly in distilled water, placed on tared cover slips, and allowed to dry at room temperature. A large number was weighed at once, to give total dry weights of 250 μg or more.

Carbon contents of measured fresh and preserved zooplankters were determined according to the wet-ashing method in Strickland and Parsons (1960), except that a Klett–Summerson photometer, with filter no. 42, was used instead of a spectrophotometer. Glucose was used as the standard, so that all carbon values are given as glucose equivalents. Preserved animals will be shown to be adequate for carbon analysis.

Although efforts were made to choose equal-size specimens when a large number were required to estimate weight or carbon content per individual, mean linear dimensions were determined from $\sqrt[3]{L^3/N}$, where L is individual length and N is total number in the sample.

Calculations of Production

Various modifications of the direct calculation of net production from growth and abundance are finding increasing use in ecology. These methods depend on the tracing of groups of cohorts of known age through time, and on the integration of numbers and biomass to give production (see review in Mann, 1969).

In the present study, production is calculated between successive sampling dates as $\overline{N}\cdot\Delta\cdot\overline{W}$, where $\overline{N}$ is mean number and $\Delta\overline{W}$ is the change in mean weight of the designated group. Since decline in numbers is more likely to be nearly exponential than linear, $\overline{N}$ is taken as the geometric mean. This helps to correct for the fact that growth in biomass between dates is also exponential, even where survivorship is linear.

Implicit in such calculations, although not generally recognized explicitly in studies of zooplankton production, is the assumption that differential, size-dependent mortality does not occur *within* a designated cohort whose growth and mortality are being traced. This problem, comparable to those raised by "Lee's phenomenon" in fisheries research, is recognized in the present study, and corrected for in a number of instances as discussed in the text.

Ecology of *Pseudocalanus minutus* (Krøyer)

Life Cycle and Population Dynamics

The *Pseudocalanus* of Ogac Lake are attributed to *P. minutus*, as has been done in other studies of copepods from the Canadian Arctic (e.g., Fontaine, 1955; Grainger, 1959). The genetically distinct large form of *Pseudocalanus* from the lake (McLaren, 1963; McLaren et al., 1966) is of special interest, and is dealt with elsewhere (Woods, 1969). The phenotypically larger individuals brought in by the tides from the cold sea are treated separately later in this paper.

Nauplii of *P. minutus* are readily identified from Ogilvie (1953) and copepodites from With (1915).

The sexes can be distinguished externally at copepodite IV (CIV). That adult females were more abundant than adult males, as in most copepods, is certainly due to the relatively short life of males, and not to a large difference in the primary sex ratio, as shown by the following combined counts from all subsamples used to follow seasonal changes in abundance.

	CIV	CV	CIV (adult)
♀	3081	1735	6320
♂	2587	1719	696

Sex ratios of CIV and CV differed significantly (χ^2 tests) from unity within many samples, perhaps as a result of slight differences in development rate of the sexes, but the great disparity only appeared among adults. The sexes are therefore best treated separately, and only the female stages CIV to adult and one half of all younger unsexable stages are shown in Fig. 2.

Clear modes in the developmental stages can be followed in Fig. 2. Approximate mean stage of development within each modal class can be calculated by dividing numbers of intermediate (minimal) stages equally between adjacent modal classes. The slopes of the broken lines joining these mean stages of Fig. 2 are then direct measures of development rate between sampling dates.

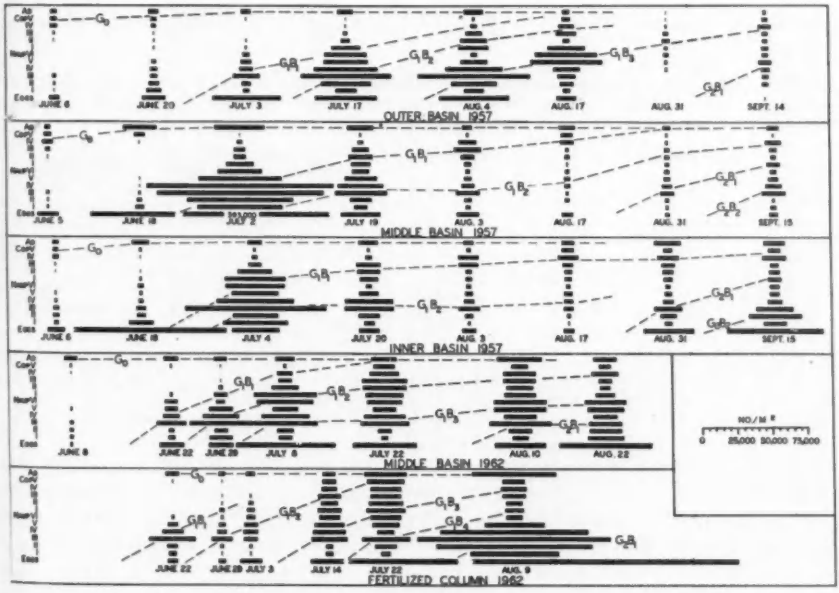


FIG. 2. Seasonal changes in numbers of *Pseudocalanus minutus* in various stages (females of copepodite IV to adult, and one-half of younger stages). Generation number is shown by subscript on G, and brood number by subscript on B (see text). The broken lines trace mean stage of development within broods and generations.

This cannot be done for the development from eggs to early nauplil; the origin of modal classes (time of 50% recruitment) is thus only estimated. Only two modal classes were inseparable on inspection. The small modal class on July 3, 1957, in the outer basin seems to have become incorporated as a "shoulder" of the main modal class (mode at nauplius III) on July 17. The patterns in the fertilized column in 1962 were less clear, and the mode at CI on July 14, which appears to be de novo, was divided equally between the two modal classes NII to NVI and CII to adult in calculating mean stages of development within these two modal classes.

The overwintered generation (G_o) was clear in each basin at the beginning of the season, and young animals appearing thereafter must have belonged to the new generation, G_1. It is now known (Corkett and McLaren, 1969) that a once-fertilized female *P. minutus* in an adequate food supply in the laboratory can produce a succession of about 10 egg sacs or clutches, each one appearing shortly after the hatching of the previous one. I believe that the distinct modal classes in G_1 represent the approximately synchronous production of egg sacs or equivalent free eggs by all the females, and therefore they are best called "broods" (G_1B_1, etc.) — a term that is often used wrongly to mean "generation" in plankton literature. The evidence is as follows. First, the calculated mean numbers in each modal class per female (Table 2) was about 20, in good agreement with the expected clutch size of about 15–20 eggs for females of Ogac Lake, based on body and egg size (McLaren,

TABLE 2. Number of young *P. minutus* per female in successive broods in Ogac Lake. Numbers in broods (modal classes) calculated by dividing numbers in intermediate stages equally between modal classes (broods), as in Fig. 2, and dividing by number of females present at the same time.

Basin and year	Brood no.	Date	Limits of modal class (brood)	Estimated clutch size per female
Outer 1957	1	July 3	NI–CII	14
	2	July 17	NI–NV	33
	3	Aug. 4	NI–NVI	27
Middle 1957	1	July 2	NI–CIV	20
	2	July 2	Eggs–NI	17
Inner 1957	1	June 18	Eggs–CII	19
	2	July 4	NII–NV	41
Middle 1962	1	June 22	NII–CI	11
	2	June 29	NII–NV	21
	3	July 8	NI–NV	16
Fertilized column 1962	1	June 22	NI–NVI	14
	2	June 29	NI–NVI	15
	3	July 14	NI–NVI	16
	4	July 22	NI–NVI	11

1965). Second, the time between the appearance of successive modal classes was of the order of a week, close to the time required for hatching of eggs (McLaren, 1966a) at temperatures of 2–7 C that prevailed in the upper waters of the lake at these times (McLaren, 1967b).

The fate of the females of G_o is not evident from the numerical data in Fig. 2, but they were distinguishable by mean size from the females of the new generation. There is no formal statistical way of distinguishing between old and new females from the polymodal size distributions in Fig. 3, as the

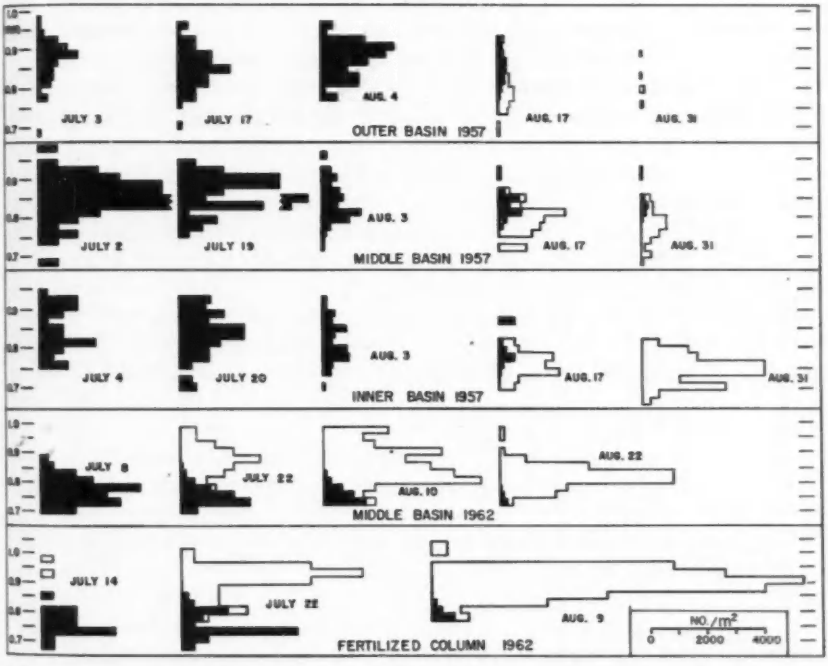


FIG. 3. Size-frequency distributions (cephalothorax lengths) of adult female *Pseudocalanus minutus* in samples from the seasons of replacement of the old generation (solid black) by the new. The size limits of the generations are estimated subjectively.

distributions within old and new females are apparently not normal. The two groups were, therefore, arbitrarily separated on the basis of subjective estimates of the size limits of the generations. It seems possible to conclude from Fig. 3 that the older generation virtually died out after mid-August of both years. For this reason modal classes appearing for the first time later in the season must be designated as members of a second generation, G_2B_1, etc., in Fig. 2. The estimated proportions of adult females in G_o and G_1 in Fig. 3 were also taken into account in drawing the lines of development of maturing broods in Fig. 2.

The timing, number, size, and ensuing fate of the various broods of G_1 can be related to phytoplankton abundance and other factors. Figure 4 summarizes the phytoplankton cycles in the upper 20 m, above which almost all the copepods, especially young stages, were found (see below under Vertical Distribution). Chlorophyll was only irregularly sampled in 1957, so counts of net phytoplankton are used. Figure 4 can only give an approximate indication of the amount of food available to the copepods; for example, the early and massive peak in the outer basin in 1957 was almost all *Nitszchia* spp., which may be inedible diatoms, and most of the later phytoplankton in all basins were the large, spiny *Chaetoceros* spp. To the extent that edible phytoplankton is associated with net phytoplankton and chlorophyll, Fig. 4 reflects the timing and perhaps relative density of food supply for *P. minutus*.

The appearance of the first brood of *P. minutus* in all instances coincided with a sharp increase of phytoplankton or chlorophyll (Fig. 4). The slightly

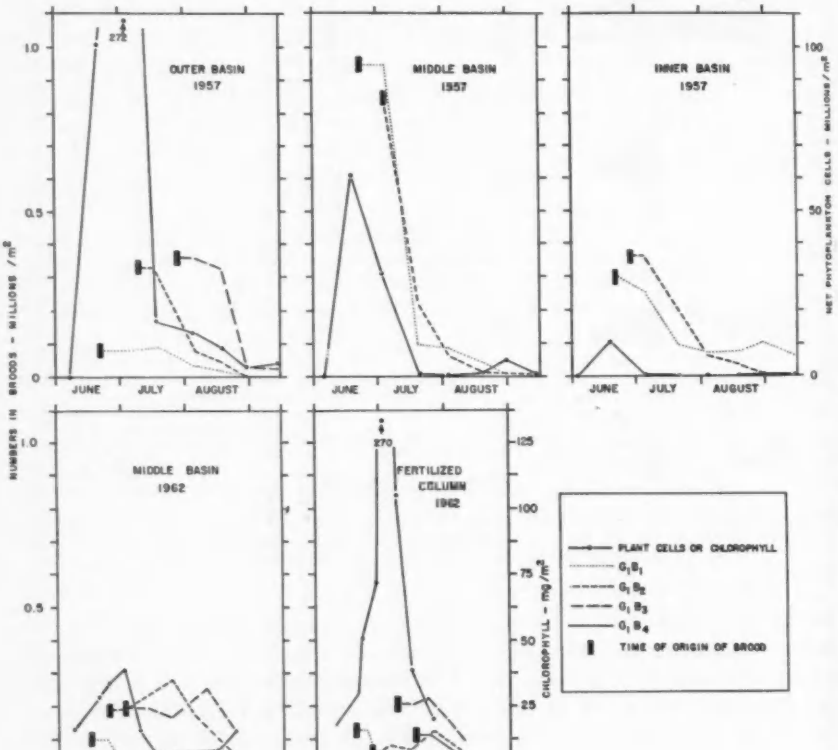


FIG. 4. Times of origin and ensuing survivorship through the seasons of successive broods of *Pseudocalanus minutus* in relation to estimates of relative density of food supply.

earlier appearance of the first brood in 1962 than in 1957 (Fig. 2) was probably due to the fact that the overwintered generation (G_o) was more advanced in development in early June, presumably because of conditions late in 1961. As pointed out above, the appearance of subsequent broods seems to have been intrinsically determined; given a certain threshold of food, broods were spawned about as rapidly as possible at the prevailing temperatures. The rate of brood production was not increased in the fertilized column. Perhaps the longer time between broods in the outer basin than in the other two basins in 1957 and the shorter time in 1962 than in 1957 (Fig. 2) were related to the cold temperatures in the outer basin and the warmer conditions in 1962 (McLaren, 1967b).

The total number of broods spawned appeared related to the timing and duration, but not the intensity of the phytoplankton bloom (Fig. 4). This agrees with observations in the laboratory (Corkett and McLaren, 1969a) that increasing food above certain threshold levels does not increase the rate of brood production, since a new sac cannot be produced before the eggs from the previous one are hatched. Thus the extra brood (G_1B_3) in the outer basin in 1957 was possible because phytoplankton was sustained longer in that shallow, nutrient-rich basin than in the other two basins. Similarly, the three broods in the middle basin in 1962 compared with two in 1957 (Fig. 2), were possible because reproduction began earlier, allowing an extra brood before decline of the phytoplankton. The effect of fertilization in 1962 was to sustain a fourth brood after reproduction had ceased in the middle basin, not to support more broods in the same time period.

The initial sizes of the broods, as pointed out above, depended on the number of females present. The small number of eggs in G_1B_1 in the outer basin in 1957 was apparently due to the fact that only a portion of the females (G_o) had matured when the first brood was produced (Fig. 2). Significantly, the enormous production of phytoplankton in the fertilized column in 1962 did not increase brood size per female (Table 2). This too matches laboratory observations (Corkett and McLaren, 1969a) that increased food does not increase clutch size.

The implication of all the above is that females in Ogac Lake reproduced at the maximal rate possible during early summer, but thereafter were thwarted by food shortage from any significant production of eggs.

The ensuing fate of the broods was affected by a number of factors. In 1957, G_1B_1 in the inner and middle basins (Fig. 2) showed more sustained development and better survival into late summer than G_1B_2, possibly because of their greater resistance as older stages to food shortage, and because of their tendency to leave the surface for cooler depths when food became scarce (see below, under Vertical Distribution). The increase in development rate of G_1B_2 in the middle basin in late August (Fig. 2) may be related to an apparent recovery of the phytoplankton (Fig. 4). All broods of G_1 showed more sustained development rate in the food-rich outer basin than in the other two basins, but the precipitous decline in numbers in the outer basin in late August did

not seem attributable to decreased food supply. The influx of 2.4 million m^3 of tidal water at this time must have displaced almost all the deeper water of the outer basin, which has a volume of 2.0 million m^3 (McLaren, 1967b). Many copepods may have been carried by overflow into the middle basin; many may also have been killed by sharp changes in temperature and salinity. The younger animals of G_1B_3 which remained on August 31 probably lived near the surface (see below under Vertical Distribution) and were less affected by the catastrophic inflow. The more sustained development rate and higher survival of broods in the middle basin in 1962 than in 1957 may be attributed to at least two factors. First, the greater freshening of the surface waters in 1962 than in 1957 led to a complex of events that sustained higher primary production near the surface (McLaren, 1969). Second, the absence of a mid-depth temperature minimum in 1962 allowed penetration of the food-rich depths by more of the older copepods when food failed at the surface (see below, under Vertical Distribution). There was little or no further improvement of survival in the fertilized column, although development of broods was maintained longer (Fig. 2, 4).

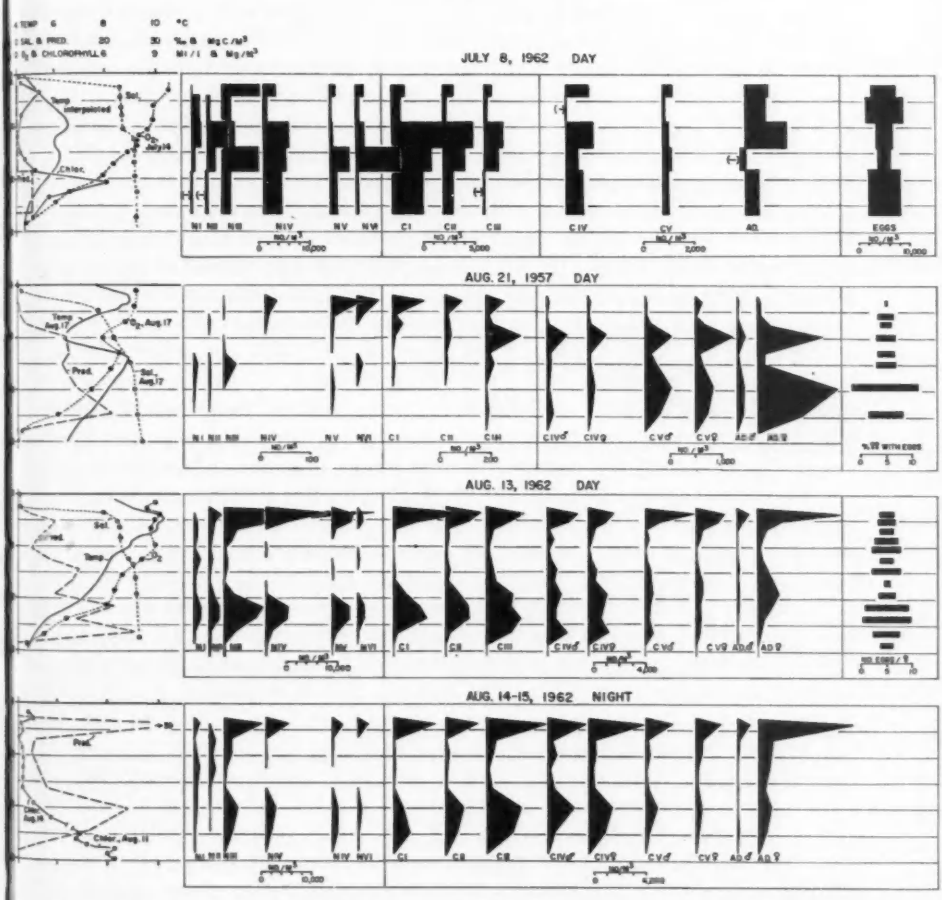
The effect of predation was not clear. Highest populations of predators occurred in the middle basin in 1962, when mortality of *P. minutus* was low (see data on predators below in appropriate sections on *Sagitta elegans* and *Aglantha digitale*).

In the last samples from the three basins in 1957 (coarse mesh only, and therefore not included in Fig. 2), on September 29, there were about equal numbers of CIV and CV, but most adults had disappeared. It is characteristic of marine calanoid copepods (e.g., Marshall and Orr, 1955) for overwintering stages to be older copepodites, presumably because younger stages have less food-storing capacity ("oil sac") and perhaps less resistance to the environment. The older copepods at the end of the seasons in Ogac Lake all belonged to the first summer generation, although different broods were involved. It is possible that some of the second generation (G_2B_1) developed sufficiently to be able to overwinter with members of the earlier generation, but this does not modify the essentially annual nature of the life cycle.

Although *P. minutus* has nowhere been studied in the detail presented here, its life cycle in other northern waters has also been shown to be annual, although a portion may mature and spawn in autumn in subarctic localities (Fontaine, 1955) or require more than a year to mature further north (Digby, 1954; Grainger, 1959). The cycle is basically biennial in the high arctic (Cairns, 1967). Carter (1965) studied *P. minutus* in Tessiarsuk, a lake on the Labrador coast very similar to Ogac Lake. There its life cycle closely resembled that in Ogac Lake, with older copepodites at the end of the season derived from G_1. Carter suggests that the autumnal burst of nauplii of G_2 developed rapidly to form the main overwintering stock, but it is just as likely that they died, to maintain a basically annual cycle, as in Ogac Lake.

Vertical Distribution

Figure 5 summarizes for four occasions the vertical distributions of the various stages of *P. minutus* and the prevailing physical, chemical, and biological conditions in the water columns. The pattern on July 8, 1962, is based on a series of vertical hauls (see Materials and Methods) and is likely only to be



5. Vertical distributions of stages of *Pseudocalanus minutus* and prevailing physical, chemical, and biological ditions in the water columns of the middle basin. Negative values on July 8 are the result of sampling errors.

approximate as the negative values at some depth suggest. The other series were made with Clarke–Bumpus samplers, and are more representative, except that the 10-mesh net used in 1957 must have allowed most nauplii and free eggs to pass through. Number of eggs per female could not be used for samples

from July 8, 1962, because of the negative value noted for adult females, and from August 21, 1957, because of the probable loss of most free eggs through the net.

On July 8, 1962, before the final wasting of ice, there were fairly distinct maxima at mid-depths, between 10 and 20 m. The upper concentration coincided with a chlorophyll peak, presaging the continuous fluorishing of phytoplankton in the halocline during summer (McLaren, 1969). However, the mid-depth maxima of all stages were in low concentrations of chlorophyll, and were above the depth of around 20 m where copepods were most abundant in summer. An "explanation" of this seasonal difference might be sought in terms of light (not shown in Fig. 5), since about the same amount of visible daylight reached 15 m on July 4 as reached 21 m on August 8, 1962 (McLaren, 1967b, fig. 9). The maxima of copepods on July 8 also tended to occur in a rather broad zone of relatively uniform temperature. It is possible, however, that light and temperature are of little importance. The pattern on July 8 may simply represent a somewhat lagging descent of the copepods in "pursuit" of the sinking phytoplankton maximum at this season; a few days earlier, the chlorophyll peak was at 15 m, near the copepod maxima (McLaren, 1969).

On August 13, 1962, the marked abundance of all stages in the halocline near the surface was again associated with a chlorophyll maximum which had somewhat passed its peak concentration there by this time (McLaren, 1969). The deeper maximum of copepods at about 20 m coincided with the upper boundary of higher chlorophyll concentrations (Fig. 5). Chlorophyll data are unavailable from these depths in 1957, but the copepod maxima at 2 and 20 m on August 21 were presumably also related to food supply, although the phytoplankton maximum near the surface may have been less pronounced in 1957 (McLaren, 1969). However, the sharp maximum of adults and older copepodites at 10 m cannot be attributed to food supply, as no chlorophyll was detected at this depth (the only depth sampled) on August 17, 1957 (McLaren, MS, 1961, table VII). The abundance did coincide with the anomalous temperature minimum at 10 m. The distinct oxygen minimum at this depth was an effect of the concentrations of copepods, and was absent on July 19, but well marked on August 4, 9, and 17. A similar O_2 depletion occurred at the temperature minimum at 12 m in the inner basin (McLaren, 1967b). This suggests that descent to 10 m occurred in 1957 in response to reduced food supply near the surface in late July and early August, at a time when there was marked mortality of younger, and apparently nondescending stages (cf. Fig. 2). Such seasonal descent commonly occurs among older copepods at the end of the productive season, and it is of interest to note that it apparently commenced in Ogac Lake with stage CIII, which is one stage before the sexes become distinguishable in this species. If the adaptive purpose of such descent is to "seek" colder waters to minimize metabolic expenditure (McLaren, 1963), then the failure to penetrate the marked positive thermal gradient at 10–15 m seems explicable. No such barrier to seasonal descent occurred in 1962, and the presence of small animals among the larger animals of deeper water suggests

that some descent from the surface had taken place by August 13 (see below, under *Size variations* of this species).

Other differences between 1957 and 1962 can be related to the patterns of brood production and survival in the two years (see above, Fig. 2, and under Life Cycles). The abundant nauplii in 1962 belonged to G_1B_3 and G_2B_1. The older nauplii in 1957 were vestiges of G_1B_2, which suffered heavy mortality in late July and early August, but the eggs and nauplii, which appear largely traceable in Fig. 5 to the females at 20 m, herald the appearance of G_2B_1. The absence of a deep maximum of young copepods in 1957, compared with 1962, was therefore a result of timing and mortality of broods, not of different depth predilections in the two years.

Figure 5 compares nighttime and daytime distributions on August 13–15, 1962. At some depths in some stages, peaks of abundance in daytime seemed to shift or disappear at night, but careful examination of Fig. 5 will show that most of these result from less complete sampling of depths at night. The adult females may have shown slight increase at ca. 10 m and decrease at ca. 20 m, but these movements, if real, only concerned a very small part of the population, It seems fair to conclude that very little if any diurnal vertical migration was occurring at this time of year in 1962.

Growth and Development

Size variations — Although food as well as temperature has been supposed in numerous studies to determine size of copepods, McLaren (1963, 1965) has argued that only temperature affects size directly, although growth and development may be thwarted by inadequate food supply. The warm temperature of Ogac Lake is certainly responsible for the much smaller size of *P. minutus*, which averaged about one-third shorter than those of the cold waters of Frobisher Bay (McLaren, 1965, see also discussion of size of allocthonous *P. minutus*, below). Because of complex thermal stratifications, Ogac Lake is a difficult environment in which to study size variation without sure knowledge of depth distributions and movements of the copepods. Therefore the data can only be used in a general way to indicate the probable roles of food and temperature. This section also demonstrates the complexity of interpretation required for a problem that is still often approached in a somewhat naive way in the literature.

Sizes of adult females (Fig. 3) have already been used to estimate the times of death and replacement of the overwintered generations of *P. minutus*. The females of G_o were almost all mature at the beginning of 1962, and presumably had developed in the warmer waters of the previous autumn. The females of G_o in 1957 averaged larger than those of 1962, because most molted at least once in the cold waters of early June. The first members of G_1 matured early in 1962, and therefore adult females were larger than the overwintered stock. Those of 1957 did not mature until the height of summer, and were smaller than those of G_o. Temperature seems a sufficient explanation for all these differences in adult size.

Figure 6 summarizes size of all copepodite stages through the seasons. Size in 1957 was generally largest in the outer and smallest in the inner basin, which conforms to slight differences in mean temperature of the basins (McLaren, 1967b). There may be a parallel effect of salinity, which is known to affect size of poikilotherms positively (Kinne, 1964). Decrease in size of younger

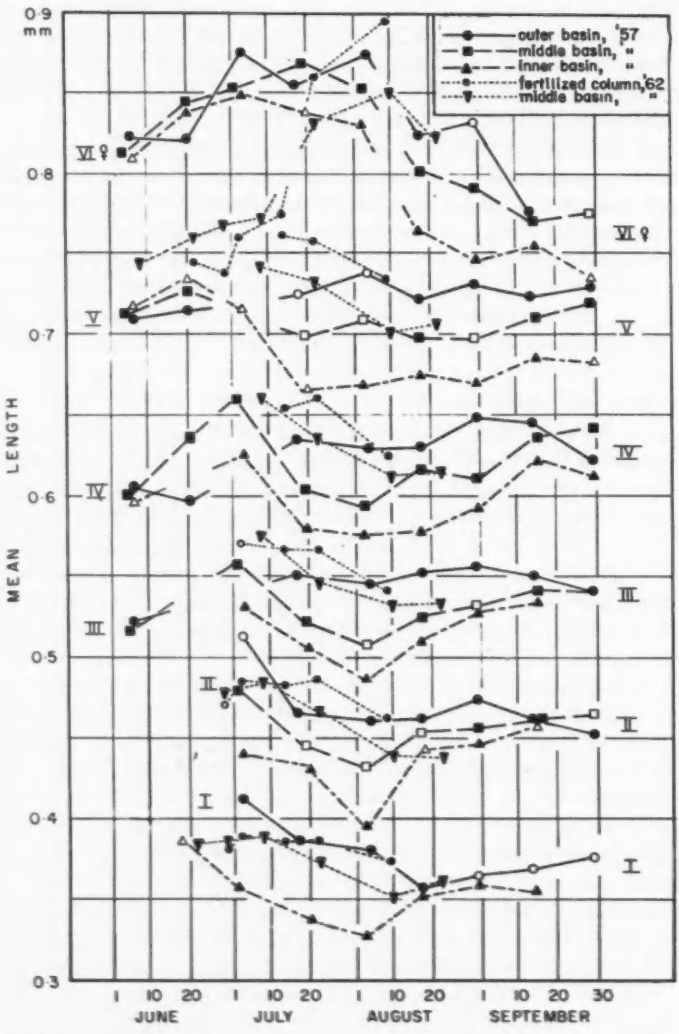


FIG. 6. Seasonal changes in mean cephalothorax lengths of copepodites (both sexes combined) and adult females of *Pseudocalanus minutus*. Open symbols based on 18–29 and closed symbols on 35 or more individuals.

stages (CI–CIII) from mid-June or early July to late July was marked in all basins in 1957, but size changed little through July in 1962. Although seasonal warming was about the same in both years, vertical temperature structure differed markedly. Copepods following the seasonal descent of phytoplankton in July (as suggested above under Vertical Distribution) would have been subjected to generally increasing temperatures in 1957, and to almost unchanging temperatures in 1962 (see McLaren, 1967b, fig. 11). Later in the season of both years the flourishing of copepods near the warm surface would have further reduced their mean size. The recovery of size in all basins during August is not so easily explained. There may have been some cooling near the surface (McLaren, 1967b, fig. 15), but not enough to restore size to values found in early July. During summer, development was very slow (Fig. 2) presumably because food was scarce. This suggests two mechanisms that may have increased mean size of copepodites. First, smaller animals may have been less resistant metabolically and suffered proportionately higher mortality. Second, smaller animals may have developed slightly more rapidly, an effect that might be more noticeable when overall development was stalled. Logically, these two mechanisms should lead to increase in size of younger stages and decrease of size of older stages; this is precisely what is shown in Fig. 6.

Although temperatures experienced by the copepods cannot be determined precisely in the stratified waters of Ogac Lake, it can be concluded that a temperature increase of some 5–7 degrees C was responsible for a 30–40% reduction in mean size of copepods in the lake compared with those in the sea. On the other hand, an increase in phytoplankton by about an order of magnitude in the upper 20 m of the fertilized column (Fig. 4) was only accompanied by size increases of at most 5%. Even here, possible differences in vertical distribution, and therefore temperature, cannot be discounted.

Seasonal differences in size were compounded by vertical differences in size (Fig. 7). In August of both years there was a tendency for animals in the colder depths to be larger. The trend was perhaps more pronounced in the more strongly stratified waters of 1962. However, agreement with temperature was by no means exact, and was probably obscured by vertical movements of copepods (see above under Vertical Distribution). For example, females in 1957 at 10 m, where the water was colder than at any other depth, were not larger than those from warmer water; this is explainable by their recent descent from the warm surface. Similarly, the increase of size of females with decreased temperature was reversed in deep water in 1962. The decrease of size in these deep-living females was accompanied by an increase in variance (indicated by length of black bars in Fig. 7); this is traceable to the presence of two size modes, the smaller mode probably representing animals that had recently descended from the surface.

Growth increments between stages — Copepods and other Crustacea are often stated to increase their length by about the same proportion at each molt, and "Brooks' Law" is an empirical generalization which states that

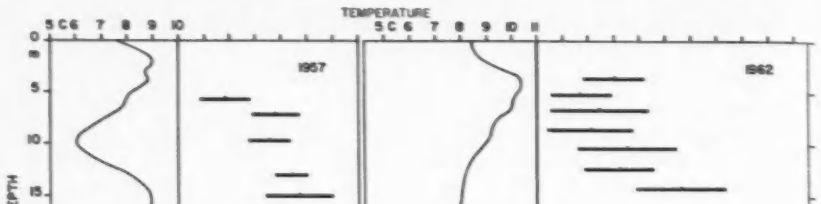


FIG. 7. Vertical differences in mean size (black bar gives 95% confidence limits of mean) of adult female *Pseudocalanus minutus* in relation to temperature in the water columns of the middle basin on August 21, 1957, and August 13, 1962.

they may increase their length by about 25% at molting. This means doubling of volume in an isometrically growing animal, and may have some theoretical interest if it implies doubling of cell number (McLaren, 1965; Rice, 1968). A constant growth proportion should of course only be looked for when conditions, especially temperature, are virtually constant. Furthermore the rule should strictly apply to individuals, and not to populations in which the inherently smallest individuals may develop more rapidly, leading to an underestimate of growth increments. For these reasons, growth increments (Table 3) have been calculated for *P. minutus* only for those periods in which copepodite development had not yet slowed down — specifically, all samples of 30 or more of each measured stage up to August 4 in the outer, July 2 in the middle, and July 4 in the inner basin in 1957, and up to July 22 in the middle basin and fertilized column in 1962 (the reasons for these choices are

TABLE 3. Growth increments between copepodite stages of *P. minutus* during periods of rapid development (see text).

Stage	No. samples	Length increment (%)	
		Mean	Range
I–II	9	24.0	(20.5–25.8)
II–III	9	18.2	(15.4–21.0)
III–IV	8	15.7	(14.2–18.5)
IV♀–V♀	4	19.4	(15.5–21.2)
IV♂–V♂	3	14.6	(13.8–15.4)
V♀–VI♀	5	20.1	(17.0–24.1)
V♂–VI♂	3	−0.2	(−0.7–0.1)

evident in Fig. 2). In addition, growth increments were calculated between CV ♀ and the distinctly larger size modes of recently matured females on June 18–20, 1957, in the outer and middle basins, the smaller size modes presumably representing females that matured earlier, perhaps in the warmer waters of early winter.

Except for older males, all stages showed about the same proportionate increase in length between molts. However, there were slight but interesting differences. The increment between CIV and CV was clearly smaller among males, and this difference between the sexes may also occur among younger stages, when males cannot be distinguished. This would account for the steadily decreasing growth increment from stages I to III, if older potential males had smaller growth increments, and also developed more rapidly to become under-represented among younger and over-represented among older stages. The growth increment of females and of younger stages combined did not approach the 25% increment implied by "Brooks' Law." However, it will be shown below that growth of *P. minutus* is not isometric, since weight increases as the 3.64^{th} power of length. This means that body mass would be doubled by a length increment of about 21%, much closer to the observed values in Table 3.

In summary, "Brooks' Law" rephrased to imply a doubling of mass between molts may have applied to female *P. minutus* during periods of rapid development, but male copepodites showed distinctly smaller increments, and adult males were no larger than stage V males.

Development rate — It is clear from Fig. 2 and the earlier discussion of life cycle that development of *P. minutus* during summer was thwarted by food shortage. It is of greater interest to consider the short periods of high food availability in spring, when development may have been proceeding at maximal, physiologically determined rates. Approximately the same periods of development (Fig. 2) were compared — the well-represented sequence between nauplii and early copepodites. To ensure that food shortage was not a factor, only those sequences that were not followed by sharp reductions in development rate were used. The following sequence in Fig. 2 meet these criteria: in 1962, G_1B_1 between June 22–29 and G_1B_2 between June 29 and July 8 in the middle basin; and G_1B_1 between June 22–29, G_1B_2 between June 29 and July 14, and G_1B_3 between July 14–22 in the fertilized column (these sequences were similarly used by McLaren (1965) where there is an error in a date for the middle basin, June 23 instead of 22); in 1957, only G_1B_2 between July 17 and August 4 in the outer basin satisfied the criteria. The resulting rates average 0.39 stages per day (SE 0.03, range 0.30–0.52). This resembles laboratory estimates for *P. minutus* from Halifax (unpublished observations) of about 0.3 stages per day between NI and CI in an excess food supply at 6 C, close to mean temperature in Ogac Lake at the time of the above estimates (McLaren, 1967b). The data from Ogac Lake, therefore, suggest that development rate of nauplii and copepodites of *P.*

minutus in the arctic, like development rate of their eggs (McLaren, 1966a), is not adaptively modified to any great extent.

One brood in the fertilized column, G_1B_2, had no apparent reduction of development rate and reached maturity about a month after birth. This, together with 5 days for development of eggs (McLaren, 1966a), may be taken as a minimal estimate of the time between generations in abundant food at the prevailing temperatures.

Weights and carbon contents — Figure 8*a* gives the relationship between mean cephalothorax lengths and carbon contents of *P. minutus*. The two values determined in the field from fresh animals do not deviate significantly from the overall regression for preserved samples.

The exponent of the length–weight relationship, like those relating length and volume of egg sacs and length and cephalothorax dimensions (McLaren,

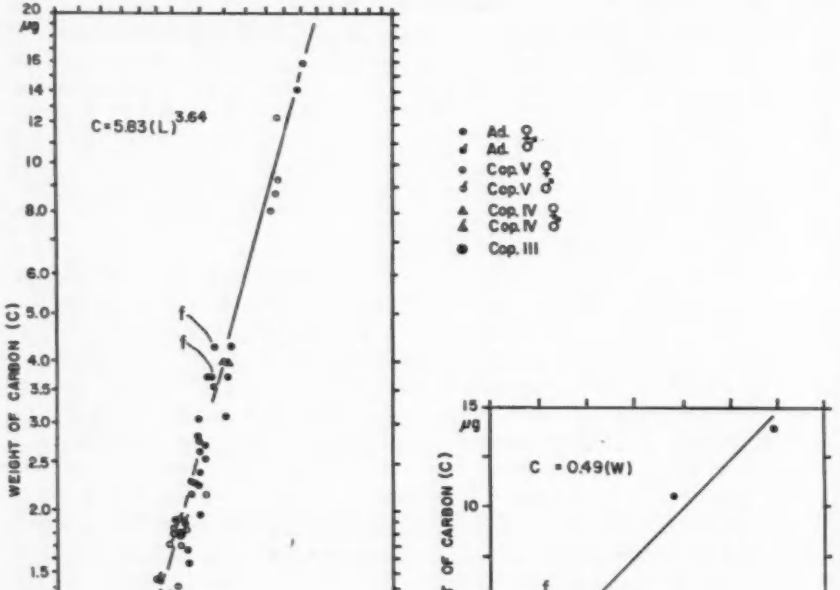


FIG. 8. The relationship between mean cephalothorax length and carbon contents of samples of *Pseudocalanus minutus*. Most points in *a* are converted from dry weights using the relationship in *b* between carbon content and dry weight per individual in samples from the same net haul. Carbon contents of two samples marked *f* were determined on fresh material in the field. All others based on preserved material. Lines fitted by least squares.

1965), is significantly greater than cubic ($P < 0.01$); *P. minutus* grows stouter as it grows longer. The relationship holds for all animals older than copepodite III, but younger animals were not weighed.

Some authors (e.g., Comita et al., 1966) have found seasonal and other variations in weight and calorific values of copepods to be independent of body length. No doubt more refined work would show similar variations in *P. minutus*, but no particular pattern could be discerned in deviations from the regression line in Fig. 8*a*. From the point of view of production studies such variations in "condition" are likely to be insignificant compared with size increases.

Two lots of preserved eggs from a very large sample from the sea off southwest Baffin Island gave almost identical dry weights of 0.30 and 0.31 μg per egg. Eggs from Ogac Lake are about one-third smaller in volume (calculated from McLaren, 1965, table 1) and should therefore weigh 0.1 μg carbon.

Young copepodites may follow the regression of Fig. 8*a*, but nauplii have an entirely different shape. A copepodite of an average length of about 360 μ (Fig. 6) should weigh about 0.15 μg C. Applying "Brooks' Law" by halving weights of successively younger stages leads to a weight of about 0.01 μg C for nauplius III — i.e., one-tenth the carbon content of an egg. This is probably not grossly in error, as young copepods characteristically live on the stored food of the egg and may not begin to feed until NIII or later (e.g., Marshall and Orr, 1955).

Production

Net production was estimated by techniques described under Materials and General Methods. Weights in carbon of adults and copepodites were estimated from Fig. 8*a*. Weights in μg of nauplii were taken as 0.05, 0.02, 0.01, 0.02, 0.04, and 0.08 for NI through NVI respectively. Since early nauplii are assumed to lose weight during development to NIII and gain thereafter, eggs, NI, NII, and NIII were all taken as 0.01 μg C in calculating the mean weight of young broods. These values are unlikely to be very accurate, but early stages have little effect on overall production estimates. Each brood was assumed to represent an equivalent number of eggs weighing 0.1 μg each, spawned on the dates indicated by the origins of the broken lines in Fig. 2. Those eggs that did not lead to successful broods were assigned to the period prior to the date of sampling. This probably gave a slight underestimate of egg production. The different sizes and different development rates of males and females among older copepodites do not produce errors, but the much greater mortality of adult males than of other stages violates the assumption of the method that no differential mortality occurs within the developing broods. This problem can be avoided by assuming that males suffer the same mortality as females — that is, by adding to the observed number of adult males so that the combined number of males in CIV, CV, and CVI is equal to the combined number of female stages in the brood. Again, the correction is probably approximate, but is much better than no correction at all. The

few examples of negative production by immature broods (e.g., G_1B_2 in the inner basin, July 20–August 3, 1957) are attributed to differential mortality, rather than sampling error, and are taken as zero production, not negative.

Overall production (Fig. 9) was estimated as 394, 496, and 341 mg C/m² in the outer, middle, and inner basins respectively in 1957. In 1962, 427 mg/m²

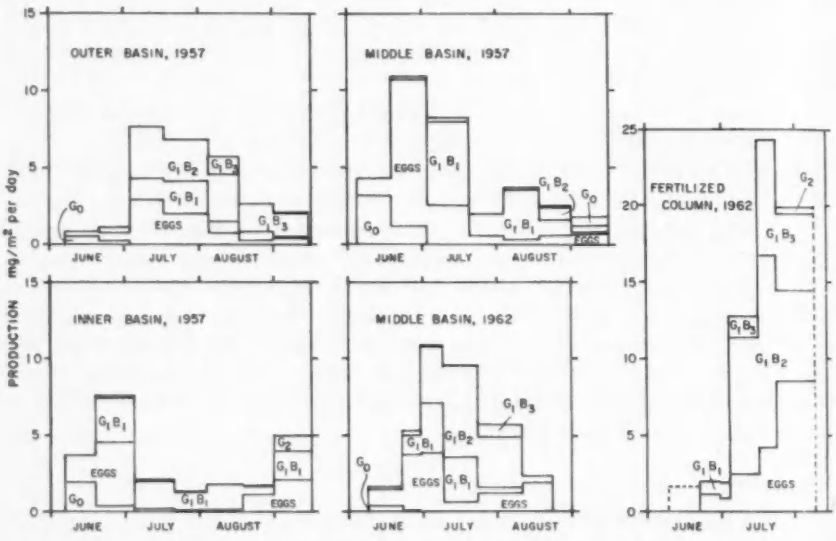


FIG. 9. Estimates of net production per day by *Pseudocalanus minutus*. Production of various broods and generations (cf. Fig. 2) shown separately.

was produced in the middle basin and 712 mg/m² in the fertilized column, during a shorter season. Assuming that the broods of G_1 in each basin made up the overwintering population, and that of G_2 simply died out (see life cycle above), another 10–20 mg/m² of production would be required to bring each brood to the condition found at the beginning of the season. Production therefore had virtually ceased by mid-September.

Much of the production at the beginning of the 1957 season resulted from growth of the overwintered adults, which supplied about 4, 13, and 9% of the year's production in the outer, middle, and inner basins respectively. Because the overwintered animals were largely mature in 1962, they contributed less than 1% of overall production in that season. Eggs were a surprisingly large fraction of production, being about 25, 45, and 33% of the season's production in the outer, middle, and inner basins in 1957, and 27% in the middle basin in 1962. The growth of the various broods supplied the rest of the production. Because of the increasing size of individuals, production was generally sustained through the season in spite of mortality losses and greatly diminished development rates (compare Fig. 2 and 4 with Fig. 9).

Fertilization and the flourishing of phytoplankton only increased production by about 1.9 times over that occurring during the comparable period in the middle basin, although a great deal more production would have taken place if the experiment had lasted longer.

ECOLOGY OF *OITHONA SIMILIS* CLAUS

Life Cycle and Population Dynamics

Copepodites of *O. similis* are of the standard cyclopoid form and readily identified. Six naupliar stages have been recognized in this genus (Murphy, 1923), although some authorities believe that other cyclopoids have five. Certainly NIV and NV are difficult to distinguish in routine counts, as they have the same setation on the antennae and NV has only two tiny, obscure extra setae on the posterior end of the body. Thus stage "NIV" in Fig. 10 possibly combines NIV and NV, and "NV" may actually be NVI. The fact that there does not seem to be an undue or regular predominance of "NIV" suggests that the possibility of grouping did not lead to serious errors of interpretation.

As in samples of *P. minutus*, adult males of *O. similis* are under-represented, presumably because they are short-lived. However, males cannot be distinguished among younger stages, and both sexes are combined in Fig. 10.

The same criteria were used to separate modal classes of development in this species (Fig. 10) as were used for *P. minutus* (see under that species), and the modal classes are similarly designated as broods of the first generation (G_1B_1, etc.). However, the broods of *O. similis* were generally not as clear, and separating them was at times arbitrary. This was especially true of broods in the earlier part of 1957, which were produced before all the overwintered females (G_o) had matured, and which appeared to suffer high mortality. For example, G_1B_1 was readily followed in the inner and outer basins, but was simply inferred in the absence of a mode on July 19 in the middle basin. On the contrary, the presence of two modes of G_1B_2 in the middle basin on July 2 and 19 was not considered to represent two broods. Later in the season, the broods were generally large and distinct, but some (e.g., G_1B_3 in the middle basin) were partly "overtaken" by later broods. Such broods were separated using the assumption that the older one was distributed symmetrically around its modal stage.

Although the first broods of the new generation evidently matured by early summer 1957 (Fig. 10), the adult females could not be distinguished by size from those of females of G_o (Fig. 11). Even at the end of the season, when all or almost all the females must have been of the new generation, there was only a very slight downward shift in size. On the other hand, the newly matured females of G_1B_1 in 1962 appeared as a distinct mode of larger size in the fertilized column on August 9, and possibly as a slight "shoulder" of larger animals in the middle basin on August 10. The mode of larger size in the middle basin on August 22 was apparently derived from advanced adults of G_1B_2. For

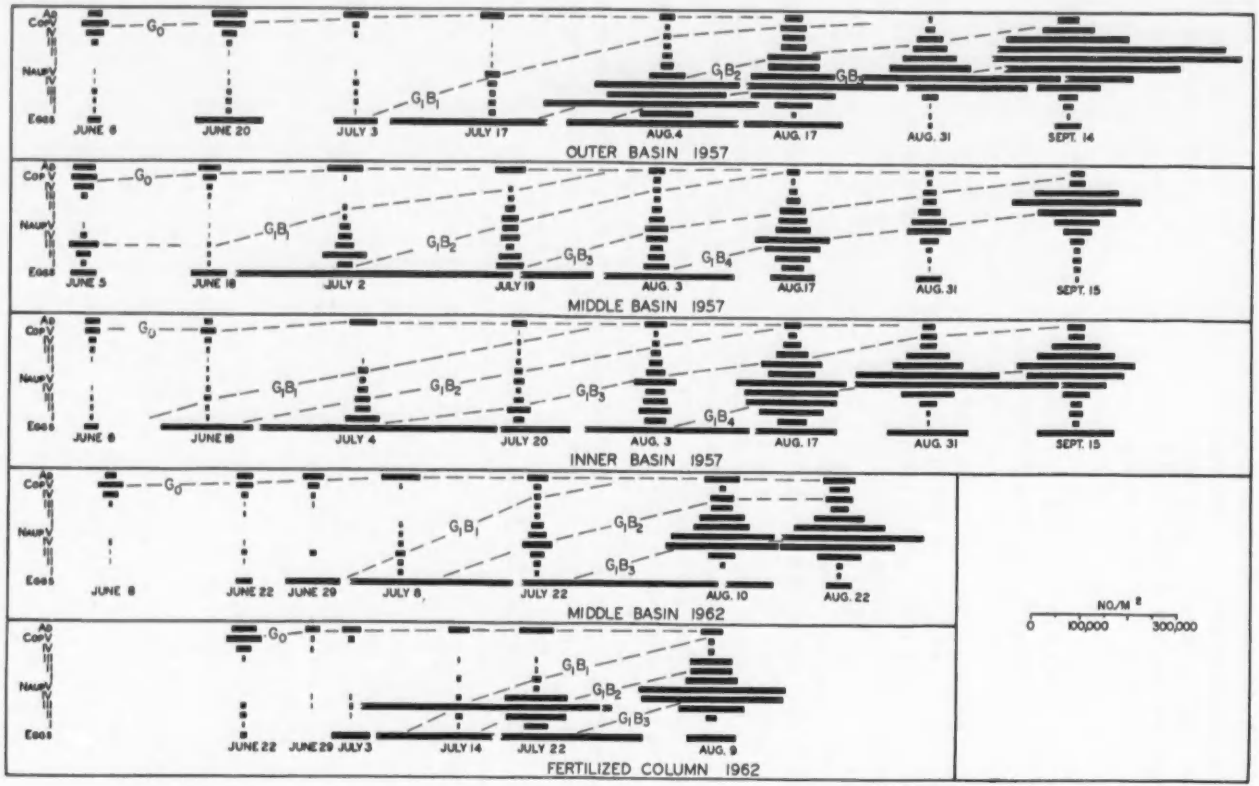


FIG. 10. Seasonal changes in numbers of *Oithona similis* in various stages. Generation number is shown by subscript on G and brood number by subscript on B (see text). The broken lines trace mean stage of development within broods and generations.

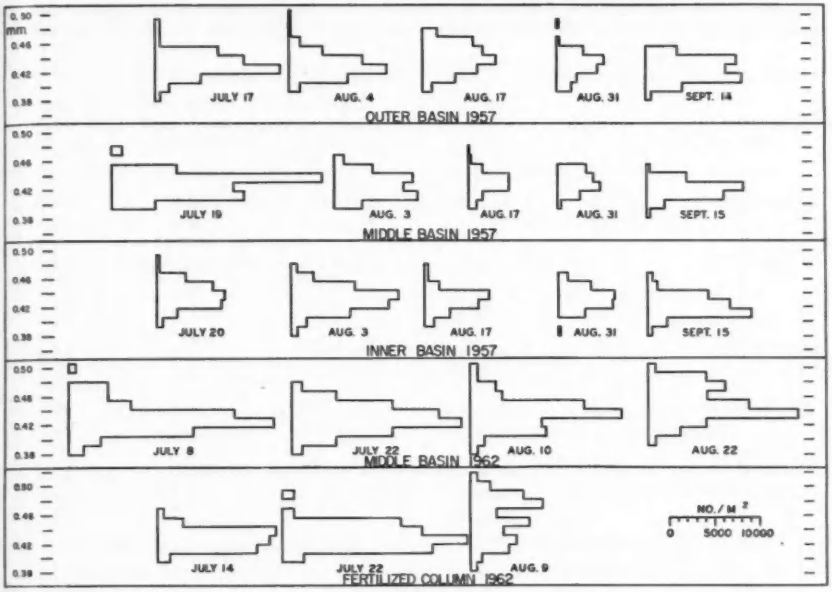


FIG. 11. Size-frequency distributions (cephalothorax length) of adult female *Oithona similis* in samples from the seasons of replacement of the old generation by the new.

purposes of calculating mean stage of development (and production estimates below), it was assumed that maturing broods were in the same numerical proportion to adults of the old generation both before and after they matured; for example, in the inner basin on July 20, 1957, G_o outnumbered G_1B_1 by 3.6 to 1, and it is assumed that on August 3 one half of CV (the stage intermediate between G_1B_1 and G_1B_2) and a portion of the adult females to make up an overall ratio of 1 to 3.6 belonged to adult females of G_1B_1. The method is very crude, but the errors are probably not large or systematic.

As in *P. minutus*, succession of modal classes in Fig. 10 suggests the almost synchronous production of egg sacs by all or almost all the females. *Oithona similis* carries paired egg sacs, which were often detached from the females, but were generally not broken up. Thus the clutch size estimated from numbers in the broods and numbers of adult females can be compared with mean numbers of eggs in pairs of egg sacs (Table 4). Table 4 deals only with broods produced after all or almost all the females of G_o had matured. Where broods appeared on successive dates, the date giving the largest estimated clutch size was chosen, on the assumption that either incomplete egg production or brood mortality would give low estimates. For example, G_1B_3 on August 3 in the inner basin leads to an estimated clutch size of 13.3 per female, but may have been incomplete, and the larger estimate of 27.3 per female on August 17 is used, even though this may have resulted from death of the

TABLE 4. Number of young per female in broods of *O. similis* and number of eggs in two egg sacs on the dates closest to the times of origin of broods in Ogac Lake. Clutch size calculated as in Table 2.

Basin and year	Brood no.	Date	Limits of modal class (brood)	Estimated clutch size per female	Contents of two egg sacs
Outer 1957	2	Aug. 4	NIII–CIII	16.6	15.6
	3	Aug. 4	NI–NIII	20.7	16.0
Middle 1957	2	July 2	Eggs–NV	15.1	16.3
	3	July 19	Eggs–NIII	8.1	13.4
	4	Aug. 17	NI–CI	33.3	15.6
Outer 1957	3	July 4	Eggs–NII	12.6	15.4
	4	Aug. 17	NI–CI	27.3	15.8
Middle 1962	2	July 8	Eggs–NI	6.0	16.2
	3	July 22	Eggs–NI	10.8	17.3
Fertilized column 1962	1	July 14	NI–NIV	14.5	12.7
	2	July 22	NI–NV	13.9	14.5
	3	Aug. 9	NI–CI	21.5	16.6

reproducing females in the interim. Considering the many assumptions and sources of error, the overall agreement between estimated clutch size (mean 16.2) and numbers of eggs in egg sacs (mean 15.5) is good, and supports the assumption that each brood was derived from the almost synchronous production of a pair of egg sacs by virtually the entire population of females.

It is also probable that the size of broods was ultimately limited by the intrinsic capacity of females to produce eggs. Although minor differences may have resulted from inclusion of some broken sacs, which were not always easily distinguished from whole ones, the overall pattern of egg sac production (Fig. 12) was similar in all basins and in both years. Small egg sacs containing 4–6 eggs were produced at the beginning of the season, generally before all the females had matured. Larger sacs of 7–8 eggs were formed during the height of the reproductive period, but there was a general falling off in egg numbers later in the season. These seasonal differences cannot be attributed to size differences (cf. Marshall, 1949), since females averaged at most about 3% shorter in early June than in July, and were either larger or smaller in July than in August in the two years (Fig. 11). It appears that 7–8 eggs were the maximal contents of an average egg sac for females of the size found in Ogac Lake even in the food-rich fertilized column, and that smaller sacs are a result of somewhat suboptimal conditions.

Survival and development of the various broods of *O. similis* (Fig. 10) differed markedly from the patterns shown by *P. minutus* (Fig. 2). In the latter, the predominant broods were born in late June and early July, and the population was much reduced late in the season. In the former, early

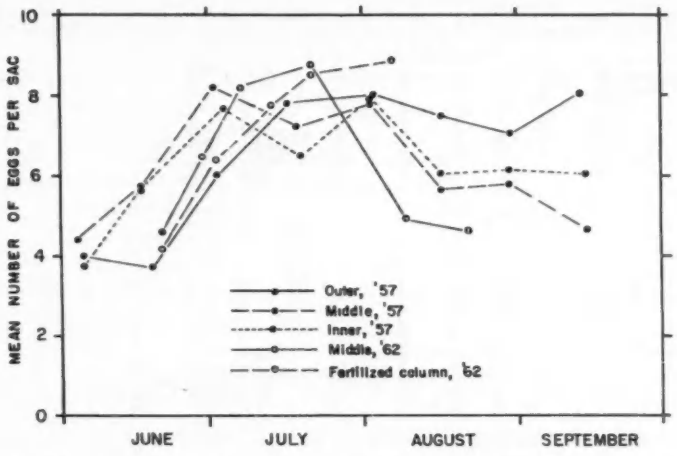


FIG. 12. Seasonal variations in numbers of eggs in egg sacs carried by *Oithona similis*.

broods were virtually eliminated, and major population increase did not occur until August. It is clear that the young *O. similis*, unlike *P. minutus*, cannot be directly dependent on the major phytoplankton flowerings of early summer. This is not surprising in view of what is known of feeding habits of the species. *Oithona similis* is probably at least partly carnivorous (Marshall and Orr, 1966). It is also noted as being abundant in sewage-rich Norwegian fiords (Wiborg, 1944), and may be a somewhat eclectic particle feeder.

The catastrophic reduction in numbers of *P. minutus* in the outer basin as a result of the tides of late August in 1957 (see under that species) is not as evident in *O. similis*. Unlike the older copepodites and adults of *P. minutus*, many *O. similis* were near the surface (see below), where they would have escaped effects of the tidal water entering the deeper parts of the basin. Nevertheless, the older stages of *O. similis*, many of which did occur deeper, were distinctly reduced in number in the outer basin, but not in the other two basins (Fig. 10).

Although the earliest broods reached maturity during summer and produced some eggs, no second generation appeared. The very large populations remaining at the end of the season clearly suffered much mortality over the winter, if they were reduced to levels found in spring. The life cycle of this species in other arctic waters has not been studied sufficiently, but is presumably annual, as in Ogac Lake.

VERTICAL DISTRIBUTION

On July 8, 1962, before the ice had completely gone from the middle basin, there was a distinct maximum of the largely mature old generation at mid-depths, and somewhat deeper maxima of young copepodites and nauplii of the new generation (Table 5). These distributions resemble those of *P.*

TABLE 5. Vertical distribution of stages of *O. similis* in the middle basin of Ogac Lake, July 8, 1962. Based on series of vertical hauls (see Materials and General Methods).

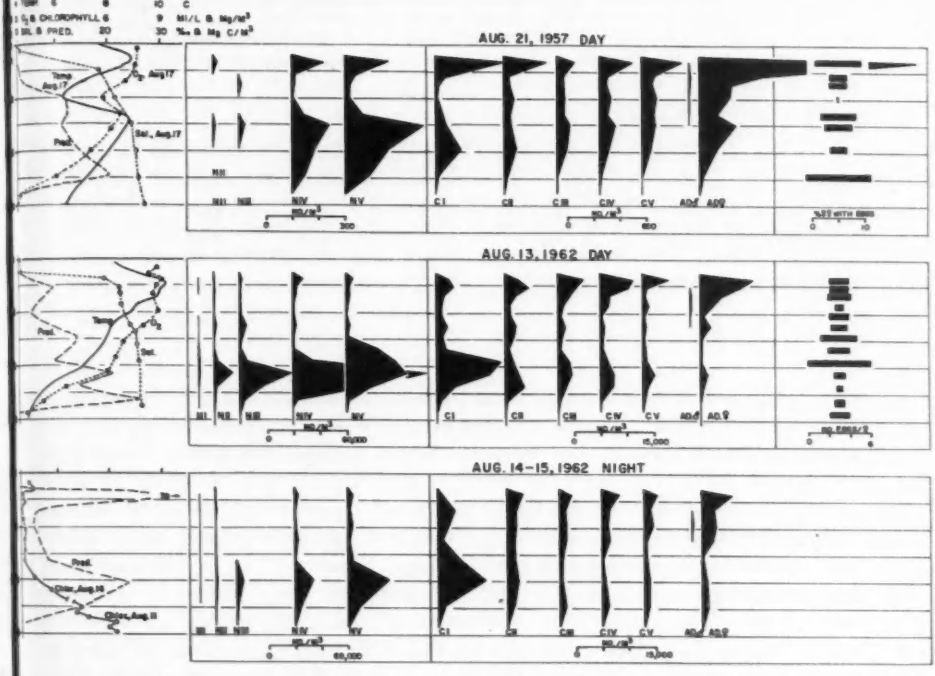
Depth (*m*)[a]	No. per m³			
	Eggs	Nauplii	Copepodites I & II	Copepodites IV to adult
2.8–4.3	1765	210	320	940
4.3–9.1	10	840	–10[b]	4360
9.1–14.0	10,130	2750	140	10,910
14.0–18.2	–310[b]	5700	1850	920
18.2–26.5	51,800	2210	370	240

[a]Based on low-water datum in summer.
[b]Negative values are result of sampling errors.

minutus (Fig. 5), although *O. similis* lacked the second distinct maximum near the surface. Curiously, there was a great abundance of free and broken egg sacs in the deepest haul — too many to have been carried by the females in the deepest stratum. If these eggs were falling into the anoxic depths, this may have been responsible for the very high mortality shown by G_1B_2 between July 8 and 22 (Fig. 10), but the cause remains obscure.

Vertical distribution during daytime in August was rather similar in both years, with maxima near the surface and in deeper water, and with a tendency for more irregular distribution of older stages (Fig. 13). Nauplii were most abundant in 1957 at about 15 m, near the temperature maximum, and in 1962 the peak was in deeper, colder water; but in each year the naupliar peak occurred at the same depth as slight maxima of most of the older stages, including females and their eggs, so that the depth at which the nauplii occurred may have depended on the depth at which they were produced by the females. The virtual absence of a naupliar peak near the surface in 1962 may have resulted from relatively greater mortality there at the time, rather than from different depth predilections in the two years. In general, the vertical distribution of *O. similis* seemed somewhat less affected by temperature than that of *P. minutus*, and showed less sharp association with the chlorophyll maximum near the surface and the high chlorophyll concentration below 20 m. This may be related to the more eclectic diet of *O. similis* and the smaller influence that temperature has on its growth (see below).

The vertical distribution of *O. similis* differed somewhat between night and day. Careful reference to Fig. 13 shows that some differences are related to less complete sampling of depths at night. This is especially true of the daytime peak in most stages at about 22 m, which would have been altogether missed at night. The decrease of numbers of copepodites near the surface at night seems real; *P. minutus* (Fig. 5) did not show this change, which therefore was not likely a result of gross sampling error. There did not appear to be a corresponding increase at any single deeper level, so the decrease near the



8. Vertical distributions of stages of *Oithona similis* and prevailing physical, chemical, and biological conditions in the water column of the middle basin.

surface is best interpreted as a result of a randomization of movement or slow, nonmotile sinking, rather than as a true "reverse" migration. This behavior might help in avoidance of predators, which increased near the surface at night (Fig. 13).

Growth and Development

Size of adult females (Fig. 11) has already been used to separate generations in 1962, but size does not vary much seasonally or between basins. A sample of adult females from the cold waters of Ney Harbour on August 17, 1967, averaged 0.497 mm in cephalothorax length, only some 8–15% longer than females in the various basins of Ogac Lake at the same season. Clearly temperature and other possible environmental variables affect size of this species far less than they do that of *P. minutus*.

For reasons given earlier (see Growth and Development of *P. minutus*), growth increments should be calculated for periods of rapid development. For Table 6, copepodites I–V were measured from the middle basin on August 17, 1957 (see Fig. 10). Because the two generations of females were difficult to

TABLE 6. Growth increments between copepodite stages of *O. similis*. Based on measurements from 30–76 individuals of each stage (except males, for which there were 21 individuals) from two samples (see text). Total length is to tips of caudal furcae, not spines.

	Mean increment in %					
	CI–CII	CII–CIII	CIII–CIV	CIV–CV	CV–CVI♀	CV–CVI♂
Total length	19.4	17.0	15.9	16.8	15.7	1.4
Cephalothorax length	10.6	9.4	10.3	12.8	14.1	2.9
Cephalothorax width	11.1	10.8	17.1	18.9	16.9	12.2

distinguish in summer, samples from June 22, 29, and July 8, 1962, were chosen to determine growth increments between CV and males and females. The short-lived males must have matured recently, under prevailing temperature conditions, but total length of females at this time was distinctly bimodal, and it was assumed that the larger modal class represented recently matured females, to be compared with CV. Table 6 shows that growth of *O. similis* was not isometric, except perhaps between CV and CVI ♀; the cephalothorax becomes progressively stouter and the abdomen proportionately longer in older stages. The overall mean increment of linear dimensions is about 15% for all stages. This does not approach the 25% length increment of "Brooks' Law," and implies a volumetric increase of about 50% between stages. Males show little increase in total length between CV and CVI, although they are clearly of a different shape.

The most rapidly developing broods (e.g., G_1B_2 in the middle basin in 1957, G_1B_1 in the middle basin and fertilized column in 1962) matured in about 1.2–1.6 months, which may be taken as a measure of the minimum time from egg to adult in this species at the prevailing temperatures.

The carbon content of 50 adult females in a fresh sample on August 26, 1962, was 0.50 μg per female. Their cephalothorax lengths were not measured, but should have averaged about 0.46 mm at this time (Fig. 11). A sample of 195 preserved females, from June 29, 1962, averaged 0.44 mm and contained 0.42 μg C per female. Considering the expected differences due to size, these two estimates of carbon content are in excellent agreement. The weighted mean of 0.44 μg C may be taken as an approximation for the average female.

PRODUCTION

Net production was determined as described in Materials and General Methods. Special problems of distinguishing modes of development, even after maturity, have been discussed above under the section on Life Cycles and Population Dynamics of this species. Measurements of egg production, the problem of accounting for the larger mortality rate of adult males, and the

treatment of "negative" production have all been dealt with in the section on Production of *P. minutus*.

In view of the small variability of size of the species, all adult females were assumed to weigh 0.44 μg C. Eggs of *O. similis* are about 50 μ in diameter, compared with 108 μ for eggs of *P. minutus* from Ogac Lake (McLaren, 1965); this implies that they might weigh $\frac{1}{10}$ as much, or about 0.01 μg C. Weights of copepodites and nauplii were calculated from weight of adult females by assuming a 50% increase in weight between stages (see above). This leads to a weight of NII of about 0.01 μg C, the same as that estimated for eggs. As in *P. minutus*, it is probable that young nauplii do not feed, and therefore lose weight during early development; thus the correspondence of weights of eggs and NII is perhaps not unrealistic.

The total production estimates are 243, 140, and 173 mg C/m² in the outer, middle, and inner basins in 1957, and 138 and 92 mg/m² in the middle basin and fertilized column in 1962 (Fig. 14). Assuming that the large populations at the end of the series gave rise after winter to populations as small as those found at the beginning of June, it is possible to estimate overwinter production;

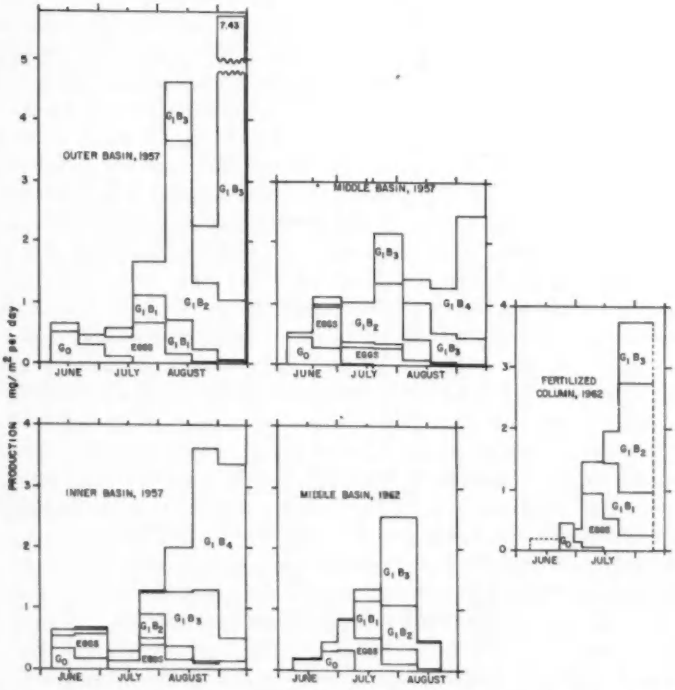


FIG. 14. Estimates of net production per day by *Oithona similis*. Production by various broods and generations (cf. Fig. 10) shown separately.

these estimates are 104, 62, and 50 mg/m² in the outer, middle, and inner basins using the 1957 samples, and 85 mg/m² using the samples from the middle basin in 1962 (it is not pertinent to calculate overwinter production for the fertilized column).

Most of the production in summer was the result of growth of the various broods. Little was contributed by production of eggs (ca. 9–15% in the various series), and less by growth of G_o (4–7%). These percentages are even less significant when overwinter production is taken into account.

ECOLOGY OF *SAGITTA ELEGANS* VERRILL

Life Cycle and Population Dynamics

Sagitta elegans is a common member of the coastal plankton of the North Atlantic and Arctic. The size-frequency distributions of *S. elegans* in the samples show clear modal classes (Fig. 15). The scarcity of adults in the fertilized column in the summer of 1962 is unreliable (see Materials and General Methods) but the series is included for completeness. Figure 15 begins in late June in 1957 because hauls from full depth were not made in early June, and adult *S. elegans* lived deep (see below under Vertical Distribution).

Like all chaetognaths, *S. elegans* is a protandric hermaphrodite. The stages used here are essentially those of Russell (1932), who distinguished them by appearance of testes and ovaries. In routine counting it was difficult to determine condition of testes. Therefore the classification was based largely on ovaries, as follows: ovaries of stage I were invisible or very faint, without obvious cellular structure; the ovaries of stage II were readily seen, but the eggs were all small and of about the same size; in stage III (adult) some of the eggs were much larger than others and the seminal vesicles were conspicuous. Maturation and spawning apparently occurred soon after eggs began to enlarge, and occasional spent animals were included as stage III.

The broken lines of Fig. 15 show the dying out of the old generations (G_o) and the estimated times of 50% recruitment (origin of broken lines) and growth of the new generations (G_1). It is assumed that most mature animals in early August belonged to the new generation, except probably in the outer basin in 1957. The large, newly matured animals appeared to die out soon after maturing. Similarly, deaths of large, mature animals at the end of the season seem to account for the slight reductions in mean size at this time. An attempt is made to trace the development of some small modal classes of young developing after the main group. These secondary modal classes are all assumed to belong to G_1, but their progress is somewhat arbitrarily indicated in Fig. 15. For example, the small modal class in the outer basin at 8 mm on August 31 is assumed to have given rise to the modal class of stage 1 at 12 mm on September 14; it is less probable that it gave rise to the mode at 5 mm by differential mortality of its large members.

Although eggs and small young later in the season can only have been produced by the new generation, there is no indication that many of these survived. The species was strongly annual in the lake, and clearly most animals

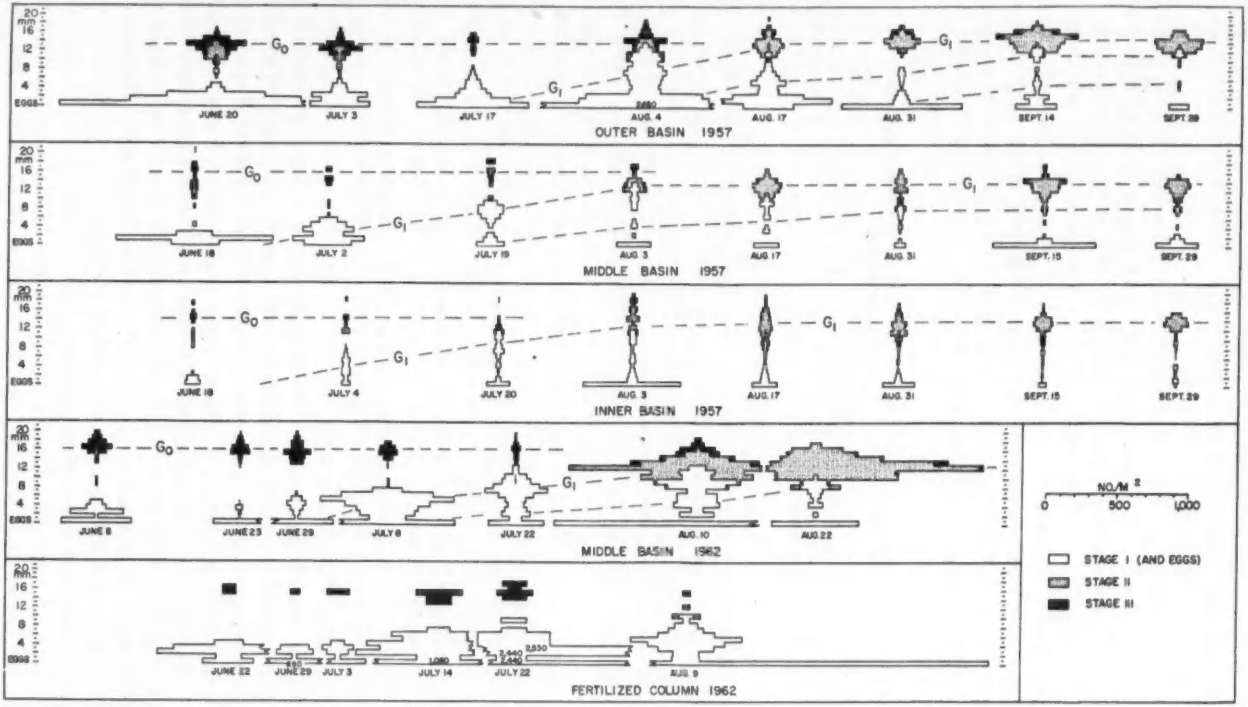


FIG. 15. Seasonal changes in size and numbers of *Sagitta elegans*. Major modal classes of the overwintered generation (G_0) and the new generation (G_1) are designated, and the broken lines trace mean lengths within these modal classes. The stages are described in the text.

had reached full size but "suspended" further development to maturity during summer when reproduction would be unsuccessful. A biennial cycle occurs in the nearby waters outside (Dunbar, 1962).

The overwintered population had largely matured when the first samples were taken in both years. Although eggs and small young were present from the beginnings of the seasons, little development of the new generations occurred until later. This was especially clear in the outer basin, where large numbers reproduced, apparently unsuccessfully, through late June and early July. The estimated mean times of recruitment of the new generations (origins of the broken lines in Fig. 15) coincide well with sharp increases of numbers of nauplii of the copepod *P. minutus* (Fig. 16), which were in fact found in the

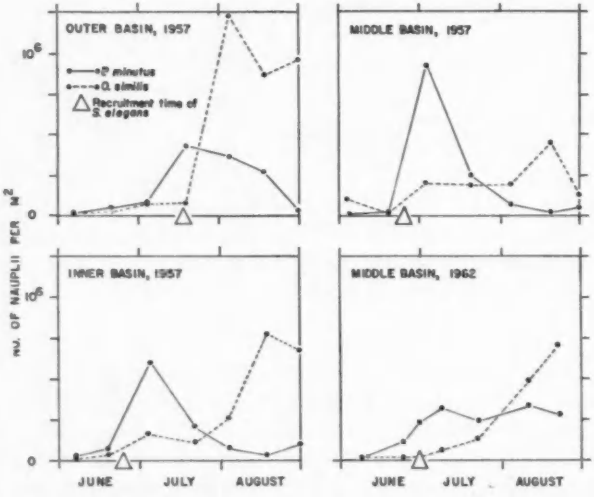


FIG. 16. Times of recruitment of new generations of *Sagitta elegans* (cf. Fig. 15) in relation to standing crops of nauplii of two copepods.

guts of tiny chaetognaths. The later abundance of much smaller nauplii of the copepod *O. similis* did not appear to support growth of young *S. elegans*. Since much reproduction occurred before and after the brief period of successful recruitment, it seems that large *S. elegans* could not detect suitable food for their young directly (guts of older animals contained copepodites and adult copepods), and that they depended on general seasonal "indicators," such as light. The few stage III animals in G_1 (Fig. 15) were perhaps induced to mature by the persisting seasonal "indicators" in early August.

The numbers of recruits of *S. elegans* were not related to the abundance of *P. minutus* at the time of recruitment (Fig. 17*a*). Rather the sizes of the new generations seemed proportional to the numbers of mature (stage III) animals (Fig. 17*b*). The potential fecundity of *S. elegans* in Ogac Lake is of

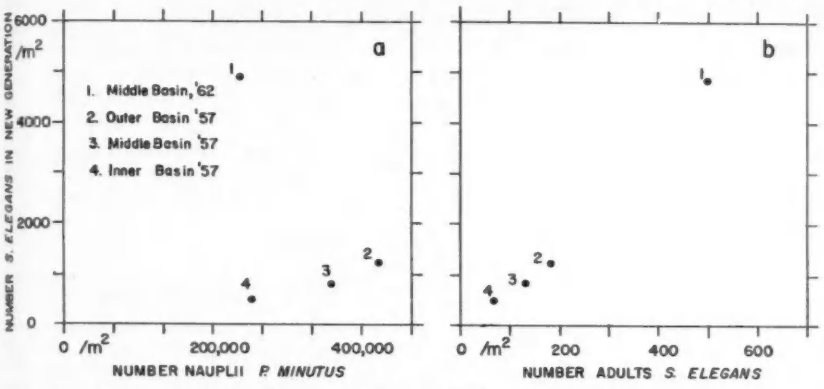


FIG. 17. Numbers of *Sagitta elegans* in new generations (means of numbers after dates of origins of broken lines designated G_1 in Fig. 15) in relation to (*a*) numbers of nauplii of *Pseudocalanus minutus* and (*b*) numbers of adult (stage III) *S. elegans* at times of recruitment of the new generations (cf. Fig. 16).

the order of 50–100 eggs (McLaren, 1966b), but only a fraction (about 10 young per adult) of this appeared as recruits. Since some animals had apparently finished spawning and died and others had not yet matured at times of successful recruitment (Fig. 15), it appears that *timing* in relation to food was much more important than *abundance* of food in determining reproductive success of *S. elegans*.

Although no significant decline in numbers of the new generations occurred during summer, the relatively small numbers of the old generations in June suggest that considerable overwinter mortality had occurred (Fig. 15). The populations in June were largest in the outer basin and smallest in the inner basin. Before considering explanations for abundance in terms of food supply, it is of interest to outline possible effects of morphometry of the three basins. Older *S. elegans* tend to migrate into deep water (see below under Vertical Migration). For example, if all older animals "sought" depths below 15 m — actively or passively, randomly or not — then populations near the surface initially of density per unit area equal to unity would become concentrated in the deeper waters of the outer, middle, and inner basins in ratios of 3.1, 1.6, and 1.3 respectively (cf. fig. 3 in McLaren, 1967b). A series of vertical hauls was made through the ice in 1962 (Fig. 18). The curves drawn in Fig. 18 are frankly interpretive, to indicate what appeared to be similar tendencies for abundance to be greatest at the boundaries of deep water in all basins. These curves have been numerically integrated with graphical estimates of the areas of each basin lying within given distances of the 30- or 20-m contours (excluding areas outside the 2-m contour, considered uninhabitable even by young *S. elegans*). This gives estimates of mean densities of 114, 58, and 49 animals per vertical net haul in the outer, middle, and inner basins — very close to the catches from the central parts of the basins (Fig. 18). It may be

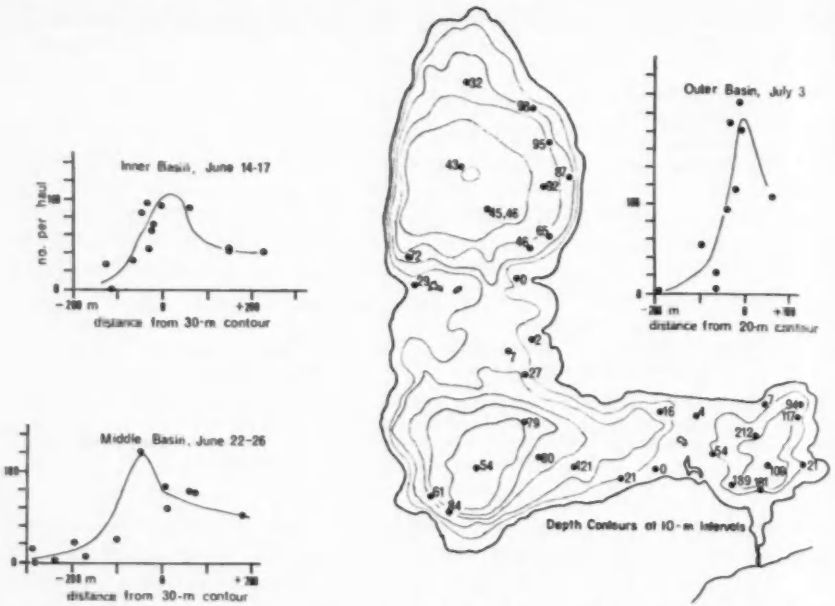


FIG. 18. Numbers of *Sagitta elegans* in the overwintered generations taken by vertical hauls through the ice by a 0.5-m no. 6 mesh net from the bottom or from anaerobic depths at the points shown (see text).

concluded that there was a distinct movement away from the shallows, perhaps after an initially more uniform distribution of young near the surface. But this movement did not apparently extend beyond the nearest "suitably" deep water; the central parts of the basins therefore continued to reflect true differences in mean population densities in the three basins.

These differences in population densities may now be compared with estimates of food supply in the three basins. An index of amounts of food available to chaetognaths during winter can be based on female copepods in samples taken in June and early July (Fig. 2, 10). Using females avoids differences due to excessive mortality of males at maturity in spring and the sampling dates are probably before much post-spawning mortality of females. The average adult *O. similis* weighs about one-eighth as much as an average adult *P. minutus*, and numbers of *O. similis* are adjusted accordingly. This index of "units of *P. minutus*" is 19,200, 39,000, 20,100 respectively in the outer, inner, and middle basins in 1957, and 17,600 in the middle basin in 1962. These do not correlate with overwintered chaetognath populations of 1325, 239, 114, and 300 per m^2 in comparable samples from June (Table 8), probably before much post-spawning mortality of chaetognaths had occurred. However, numbers or biomasses per unit *area* are probably inappropriate measures of availability of food to the chaetognaths. Older *S. elegans* probably

TABLE 7. Estimated numbers of overwintered *S. elegans* per m^2 in the deepest parts of the three basins of Ogac Lake on comparable dates in 1957 and 1962. Based on the regular seasonal series of samples, as well as on 0.5-m no. 0 net (see Fig. 18), assuming the net to be 100% efficient.

		June					
Basin and year		8	13–14	17–20	23	29	July 3–4
Outer	1957			1325			853
	1962		1406[a]				605
Middle	1957			239			134
	1962	608		300	329	468	
Inner	1957			114			123
	1962		253	239			

[a]Mean of three samples on June 13 (not shown in Fig. 18), *not* in the deepest part of the basin.

TABLE 8. Numbers of stage II and III *S. elegans* taken by single vertical hauls in 1962 from various depths to the surface with a 0.5-m no. 0 net. Hauls in each basin made in areas within a few meters.

Depth (*m*)	Outer basin, June 13 (*bottom 18 m*)	Inner basin, June 14 (*anaerobic at 32 m*)
3	0	–
6	8	0
10	22	33
15	216	20
18	337	26
20		27
23		38
28		45
35		46

wintered deeper than the bulk of their prey (see below, under Vertical Distribution), especially in the deeper middle and inner basins. It is noteworthy that the overwintered populations of 1962 were larger than those of 1957 in the middle and inner basins, but about the same size in the outer basin (Table 7). The strong positive temperature gradients in the winter of 1956–57 (see fig. 11 in McLaren, 1967b) may have inhibited pentration of *P. minutus* into the deeper waters of the middle and inner basins (for discussion of this effect of temperature see section on Vertical Distribution of *P. minutus*). Thus *S. elegans* may have been thwarted from access to much of its principal prey during that winter, explaining the low populations of *S. elegans* in June, in spite of high indices of food supply.

Vertical Distribution

The patterns of vertical distribution were similar in the summers of 1957 and 1962 (Fig. 19), and appeared to reflect an ontogenetic ascent of young animals after they had hatched from eggs produced in deep water and an

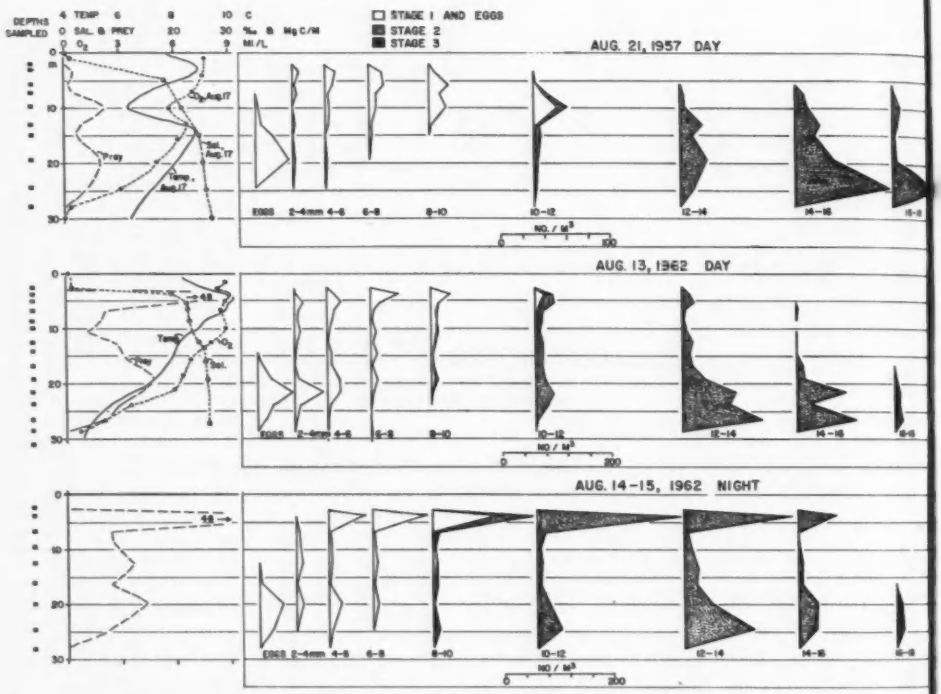


FIG. 19. Vertical distributions of length classes of *Sagitta elegans* in relation to prevailing physical, chemic biological conditions in the water column of the middle basin. Stages defined in the text.

ontogenetic descent with the onset of sexual differentiation. The tendency for older animals to be found in deeper waters has been widely reported for this species. In Ogac Lake this movement carried larger animals into depths of low oxygen and relatively small potential food supply.

Vertical hauls made in June 1962 suggest that almost all large, overwintered animals were near the bottom of the outer basin, but that many occurred at mid-depths in the inner basin (Table 8). This does not seem attributable to different limiting depths in the two basins. Possibly animals in the inner basin, where the reproductive season was more advanced (cf. Fig. 16), had risen into shallower waters to spawn. Unfortunately, no comparable series was made in the middle basin.

There was clear evidence of vertical migration at night into copepod-rich waters near the surface of the middle basin in 1962 (Fig. 19). To test the possibility that large animals were avoiding the net during the day, a horizontal haul was made at midday on August 15 with the Clarke–Bumpus sampler at much higher speed (ca. 4–5 mph), with a coarser net (no. 6) for greater filtering efficiency, and at about the same mean depth (estimated 3.9 vs. 3.6 m). The number of stage II animals was in fact smaller (ca. 7 vs. 27 per m^3) than in the sample taken with a finer net (no. 20) at slower speed (1–2 mph) in the series of August 13. Only stage II and possibly larger stage I individuals appeared to migrate (Fig. 19). It should be noted that the samples taken at night were widely spaced, so that the impression of large numbers of migrants near the surface may be misleading if the animals were concentrated in a very narrow stratum. Similarly, it cannot be assumed that the peak at 21.4 m during the day consisted of descended migrants, because no samples were taken at night between 19.9 and 24.4 m.

Although the animals were generally concentrated either near the surface or at depth, the distinct peak of large stage I animals at 10 m in 1957 deserves mention. Whether these were briefly "trapped" in the temperature minimum during ontogenetic descent, or whether they were diel migrants, they do suggest some significance of temperature in terms of vertical migration (cf. McLaren, 1963).

Growth and Development

The effects of temperature on size of *S. elegans* have been discussed elsewhere (McLaren, 1963, 1966b). The small size of adult *S. elegans* in Ogac Lake (mean 14.3 mm in length compared with 37 mm in the waters of Frobisher Bay) is clearly an ecophenotypic response to temperature. The species is annual in the lake, but biennial in the sea outside. Although it has been argued (McLaren, 1966b) that an annual cycle and smaller size, which involve much reduced fecundity, are ill-adapted to the arctic environment, *S. elegans* is clearly very successful in Ogac Lake. Apart from the possibility that Ogac Lake may offer freedom from predation and competition, it may be that the successful maintenance of an annual cycle for these arctic-adapted populations can only occur within the narrow range of warm temperatures in Ogac Lake. Support for this view comes from samples taken from another landlocked fiord, Winton Bay on the east coast of Baffin Island. This "lake" (see description in McLaren, 1967b) is intermediate in temperature between Ogac Lake and the sea outside. A series of vertical hauls in August 1964, with a net shown to be 100% efficient in Ogac Lake (see under Materials and General Methods), showed that *S. elegans* was much scarcer than in Ogac Lake, and that the larger animals (mean length 21.4 mm) were mature and spawning at this time (Table 9). The colder temperatures of Winton Bay may have delayed development and caused maturation at a time of year when the biological season (production of nauplii of copepods) was inappropriate. This

TABLE 9. Numbers per m^3 of *S. elegans* in the outer basin of the landlocked head of Winton Bay, 1964. Based on single vertical hauls with a 0.5-m no. 6 net, 100% efficient. There was no size overlap between stage I and II.

Date	New generation		Old generation	
	Eggs	Stage I	Stage II	Stage III
Aug. 7	28	143	44	56
15	0	22	11	17
28	215	6	6	22

would account for the much lower population of *S. elegans* in Winton Bay than in Ogac Lake.

The relationship between length and carbon content (Fig. 20) is not significantly different from cubic, suggesting that growth is isometric between at least 5 and 17 mm. The carbon content of 57 fresh eggs was 1.16 μg per egg.

PRODUCTION

Net production was determined by integration of numbers (Fig. 15) and changes in weight (from Fig. 20). The broken lines in Fig. 15 indicate

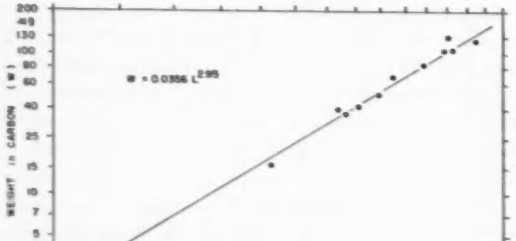


FIG. 20. Relationship between carbon content and length of fresh *Sagitta elegans*. Line fitted by least squares.

those modal classes for which production was calculated separately. Sometimes, as in the middle basin between August 17 and 31, 1957, separation of modal classes avoided large negative values of production caused by apparent sampling error. Even so, examples of negative production did occur as a result of apparent reductions in mean weight of animals in the new generations in summer. These anomalies seemed to result from the maturation, spawning, and death of the larger individuals, as discussed above (see under Life Cycle and Population Dynamics of this species). Therefore, estimates of production in summer assume the stage III animals all die out between sampling dates.

As another approximation it is assumed that eggs and small, nondeveloping young (not designated as modal classes in Fig. 15) on each date were all produced in the preceding period. These eggs and young add very little to overall production, and the approximation is justified.

The great bulk of production (Fig. 21) is traceable to the period immediately after recruitment of the new generation (91%) and relatively little

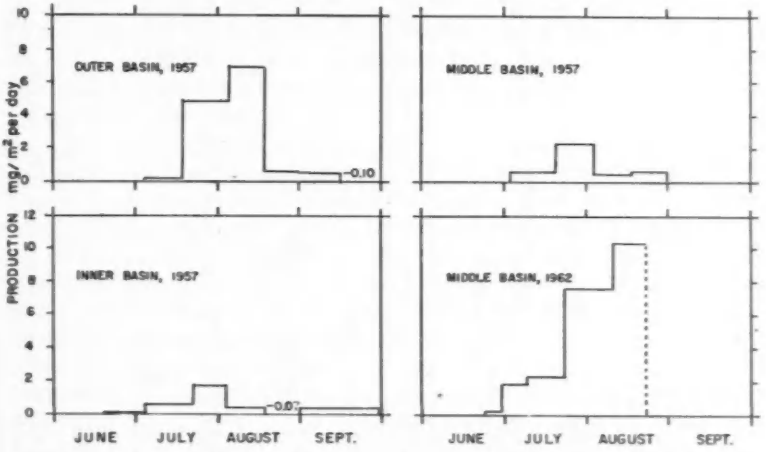


FIG. 21. Estimates of net production per day by *Sagitta elegans*. Negative values result from sampling error.

to growth of overwintered generations (1%), to eggs and nondeveloping young (ca. 1%), or to the smaller modes of young in summer (8%). Total carbon production was about 196, 62, and 49 mg/m² in the outer, middle, and inner basins respectively in 1957, and 318 mg/m² in the middle basin in 1962. These amounts of production do not parallel estimates of either production or standing crops of copepods (cf. Fig. 2, 9, 10, 14), but clearly production of *S. elegans* was closely related to abundance of the new generation, which in its turn reflected the number of adults present at the time of recruitment of the generation (cf. Fig. 17*b*).

ECOLOGY OF *AGLANTHA DIGITALE* (MÜLLER)

LIFE CYCLES AND POPULATION DYNAMICS

This species is a widespread trachymedusan of the Northern Hemisphere. There is no hydroid stage, and the species is thus truly holoplanktonic.

The three ratios of gonad length to bell height given in Fig. 22 may be taken as defining immature, maturing, and breeding animals. Spent individuals, which were often dead and decaying, were included in the adult category (gonad > 10% of bell height).

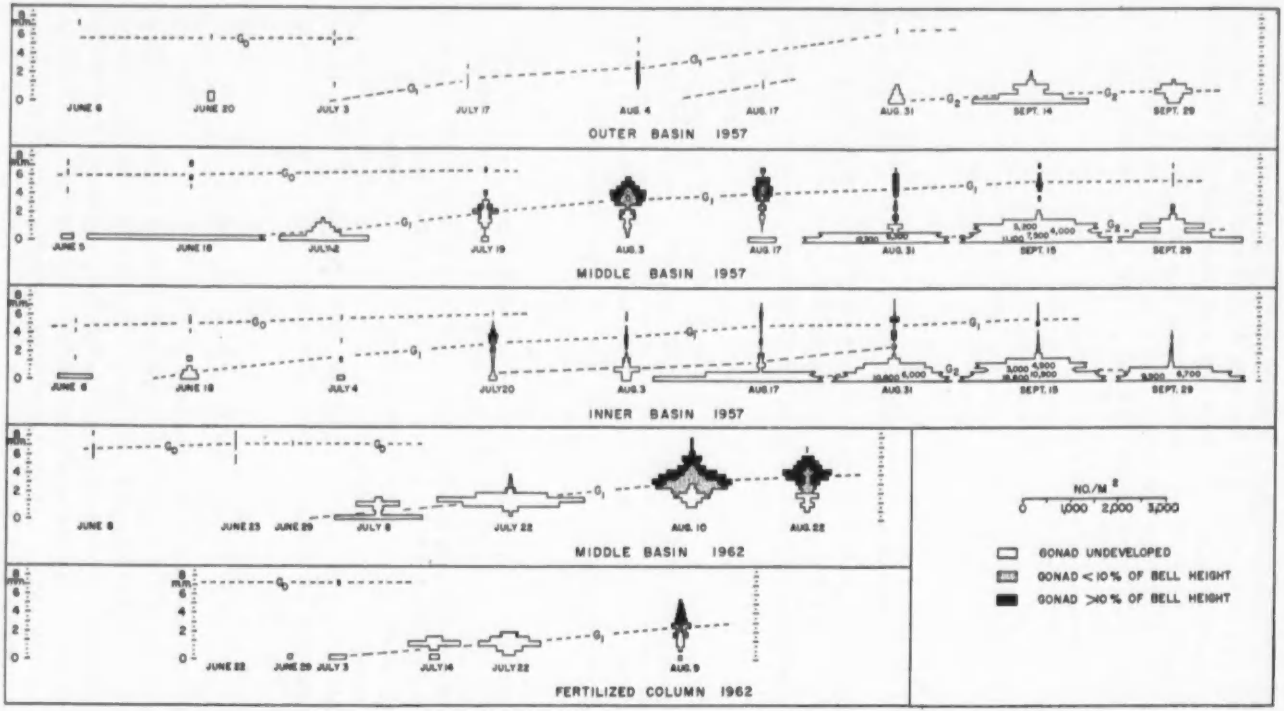


FIG. 22. Seasonal changes in bell height and numbers of *Aglantha digitale*. Major modal classes of the overwintered generation (G_0), the first summer generation (G_1), and the second summer (overwintering) generation (G_2) are shown, and broken lines trace changes in mean size within these modal classes.

Overwintering animals (G_o) were scarce, especially in the outer basin in 1957, where only four adults were taken in the earliest series of samples. These adults of G_o were clearly responsible for production of the modal classes of the summer generations, G_1. The apparent disappearance of G_o before the advent of G_1 in 1962 may have been due to the incomplete retention of the smallest animals; eggs and planulae were not recognized, and the youngest specimens taken by the fine-mesh nets were mere discs without tentacular buds and less than 0.1 mm across. Apparent uneven abundance of these very small animals later in the season may have been related to degree of clogging of the net by phytoplankton, etc. Small numbers and patchiness of distribution may also have contributed to apparent gaps in sample series of larger specimens.

Unlike the first new generation of any other macroplankter in the lake, those of *A. digitale* clearly matured, spawned, and died out in summer, and gave rise to another new generation, G_2. From the rapid reduction of G_1 in summer, it seems that few mature animals on a given date survived to the next sampling date. Apart from a few animals spawned early in the inner basin (undesignated modal class in Fig. 22), which may have matured and died by late September. there was very little development of G_2. It is assumed that the great numbers of young died, leaving only a small number of older individuals to develop during winter. It seems unlikely that another generation was produced in winter.

The life cycle of *A. digitale* in the colder waters outside the lake is probably annual. Grainger (1959) found a few large animals with immature gonads in Foxe Basin in winter, but took only small animals in summer. Kramp (1942) found large animals with fully developed gonads in summer off West Greenland. (See discussion of gonad size below, under Growth and Development.) In the eastern North Atlantic, there may be several generations per year (Russell, 1953).

The exact times of appearance of G_1 are difficult to estimate because of gaps in the samples and the dates of 50% recruitment are somewhat arbitrarily indicated by the origins of the broken lines in Fig. 22. These dates are not closely related to peak numbers of nauplii of the two copepods (cf. Fig. 16). The tiny young of *A. digitale* may require smaller food. The recruitment times do coincide well with the peaks of phytoplankton cells or chlorophyll (cf. Fig. 4). The apparently small numbers of larger animals derived from the enormous production of young in G_2 may reflect shortage of phytoplankton food late in the season.

Unlike *S. elegans*, adults of *A. digitale* live at depths close to the greatest concentration of potential food organisms (see below, under Vertical Distribution of *A. digitale*). There was, however, no correlation between numbers of adult *A. digitale* at the end of winter (means of 11, 90, and 38 per m^2 in the first two samples from the outer, middle, and inner basins in 1957, and 18 per m^2 in the middle basin in 1962) and indices of food available in winter (19,200, 39,000, 20,100, and 17,600 "*P. minutus* units" respectively; see derivation of this index under Life Cycle and Population Dynamics of *S. elegans*).

The abundance of G_1 in summer is best estimated from the two samples in each series after the time of 50% recruitment and before large numbers had matured and died (see Fig. 22). The estimates are 180, 2950, 350, and 8300 per m^2 in the outer, middle, and inner basins in 1957, and the middle basin in 1962. The figures do not correlate with the abundance of adult animals in spring (see above), nor with differences in phytoplankton or naupliar crops (cf. Fig. 4, 17*b*), and the control of recruitment remains obscure.

Vertical Distribution

Vertical distribution of *A. digitale* on August 21, 1957, suggests that most young were born at mid-depths and underwent an ontogenetic ascent, followed by descent (Fig. 23). No small animals were found at mid-depths in the summer of 1962, but the vertical hauls of July 8 in that year showed a concentration of young (all < 1.5 and most < 0.5 mm in bell height) at 10–20 m depth, as follows (depth uncorrected for standard datum; negative value from sampling error):

Depth (*m*)	3–5	5–10	10–15	15–20	20–27
No./m^2	45	25	220	640	−210

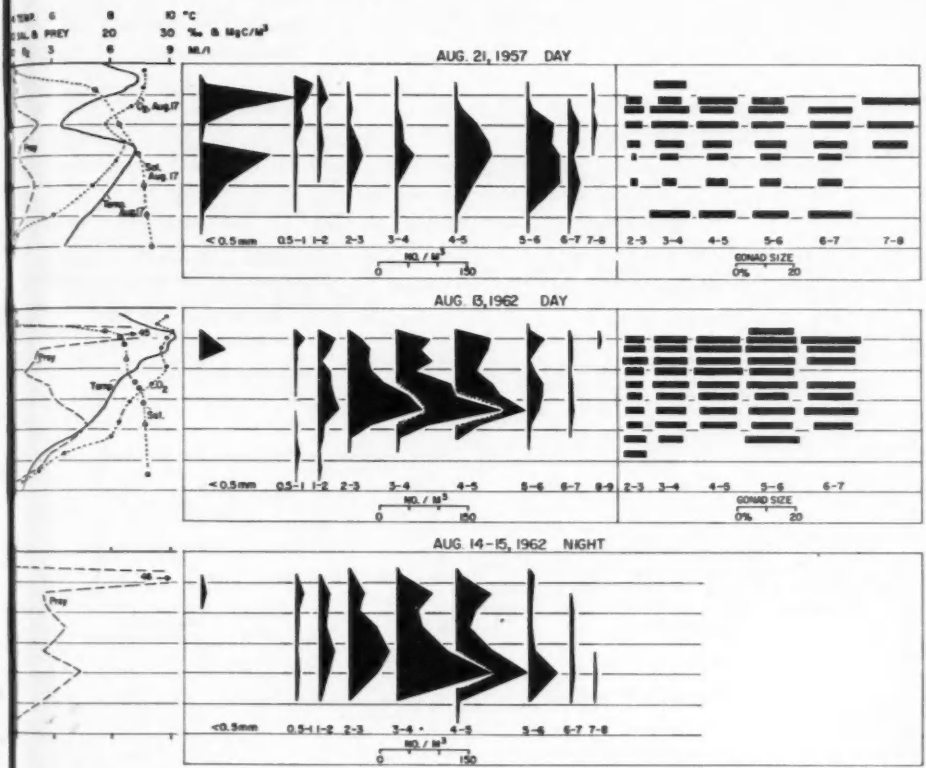
Although near-surface peaks of numbers occurred in both summers (Fig. 23), these were considerably deeper than the peaks of copepods and chaetognaths (Fig. 5, 13, 19). The limiting factor near the surface does not seem to have been temperature, but may have been low salinity. Whatever the direct cause, it had the effect of keeping *A. digitale* deeper than the concentrations of potential food supply nearer the surface. The maxima of larger animals at 10–20 m generally occurred at depths with substantial food, but well above the maxima of *S. elegans*.

Close comparison of the day and night data of 1962 suggests a small amount of descent occurred at night. This is especially clear in the appearance of a peak at 19–20 m, which depth was well sampled by day and night. The change has the appearance of a passive descent, rather than an active migration, since it only involved changes of a few meters.

Growth and Development

The reduction in size of *A. digitale* in Ogac Lake is greater than for any other zooplankter studied there. A sample of 22 adults from the tidal inflow into the lake on August 17, 1962, averaged 19.3 mm in bell height, compared with a mean of 4.3 mm for adults in the middle basin of the lake on August 22. This species has two generations annually in the lake (Fig. 22), presumably because its development rate is also greatly affected by the high temperatures. Large seasonal and local differences in size are well known in this species (Russell, 1953).

The same allometric relationship between adult gonad length and bell height seems to apply to large and small animals (Fig. 24). This relationship



Vertical distributions of size classes and relative gonad length (as % of bell height) of size classes of *Aglantha* in relation to prevailing physical, chemical, and biological conditions in the water column of the middle basin.

seems widely prevalent, for Russell (1953) states that mature *A. digitale* in the eastern North Atlantic have gonads 5–7 mm long when the bell is 16–18 mm high and 0.75–1.0 mm long when 5–6 mm high; this matches the relationship in Fig. 24.

Consistent differences in relative size of gonads of animals captured at different depths were found in 1957, but not in 1962 (Fig. 23). Length of mature gonads should be the same for animals of a given size (Fig. 24) and it is probable that the proportionately smaller gonads of animals at about 15 and 20 m in 1957 had not yet matured. This may be related to the smaller prey biomass at these depths (Fig. 23).

The relationship between bell height and weight implies isometric growth for larger animals (Fig. 25). However, the few carbon measurements for animals smaller than 1.6 mm clearly deviate from this relationship. The exponent of about 1.0 suggests an increase of height without radial growth. This is in fact observed, as the young animals change shape from a flattened disc to the

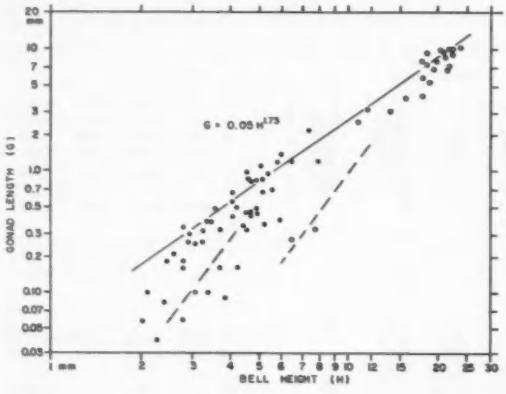


FIG. 24. Relationship between gonad length and bell height of individual *Aglantha digitale* from the waters of Frobisher Bay flowing into Ogac Lake on August 17, 1962 (open symbols) and the middle basin of the lake on August 10 and 22, 1962 (solid symbols). The unbroken, eye-fitted line represents the relationship for fully grown animals, and the broken lines suggest possible growth trajectories for animals in and outside the lake.

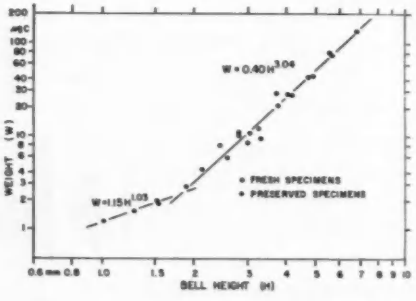


FIG. 25. Relationship between carbon content and bell height of *Aglantha digitale*. The two lines are fitted by least-squares to points for animals larger and smaller than 1.6 mm respectively.

more elongate form of the adult. Younger animals may grow isometrically in the disc form. Gonads become visible when isometric growth begins, at about 2 mm (Fig. 24).

PRODUCTION

Net production of *A. digitale* was calculated from the length–weight relationship (Fig. 25) and changes of size within modal classes in Fig. 22. A number of further assumptions and approximations were necessary.

(1) Carbon contents of very small animals were estimated from shape changes. Those <0.07 mm were taken as 0.001 μg C, 0.07–0.15 mm as 0.01 μg C, and 0.15–0.5 mm as 0.6 μg C. Accuracy is unimportant, since these small animals add very little production.

(2) Production by the small numbers of animals in G_0 at the end of winter, some of which had not in fact matured, was considered negligible.

(3) All adults of G_1 were assumed to die between sampling dates in summer. This is an arbitrary alternative to assuming that all survive, which is clearly not so (Fig. 22); probably, in fact, most do die.

(4) Because of the apparent gap in the sample from the outer basin on August 17, 1957, production was estimated using size changes between August 4 and 31.

(5) The large numbers of young on August 31, 1957, were assumed to have given rise to the modal classes at 0.5–1.0 mm in mid-September; smaller animals in mid-September then represent additional production. Reduction of size in late September is attributed to differential mortality, and zero production is assumed for G_2 between middle and late September.

Although little production occurred after mid-September in 1957, production doubtless occurred after the sampling season in 1962 (Fig. 26). Assuming

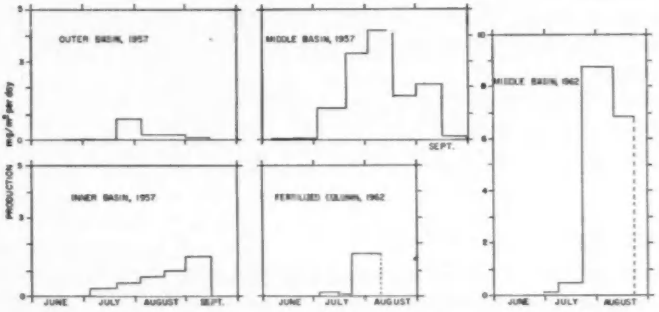


FIG. 26. Estimates of net production per day by *Aglantha digitale*.

that all immature animals present on the last sampling dates in 1962 (Fig. 22) developed to equal in size the mature animals on these dates, then 58 and 25 mg C/m² can be added to the middle basin and fertilized column respectively. A further 17 mg C/m² might be added to both — an amount equivalent to production of the large numbers of young in G_2 in the middle basin in 1957. If only a few animals developed through winter, equal to the mean number in all overwintered populations (G_o) in early June, then production can be approximated by assuming growth from 1 to 6 mm during this period. This adds only 5 mg C/m² to the estimates.

The estimates of annual production then stand at 13, 193, 57, and 263 respectively for the outer, middle, and inner basins in 1957, and the middle basin in 1962. These strikingly different values are obviously correlated with the abundances of G_1, which do not themselves seem explicable in terms of food supply or size of adult stock in G_o (see above). It is clear that *A. digitale* did not increase its production in the fertilized column. Indeed, perhaps because a relatively small number of adults were trapped initially in the column, the summer production was only 32 mg C/m² compared with 101 mg in the middle basin during the same period.

ECOLOGY OF OTHER RESIDENT ZOOPLANKTON SPECIES

Many species occurred only rarely in the plankton samples or were too small to contribute much to secondary production in the water column. Some of these species were clearly brought in by the tides and were incapable of prolonged existence in the lake; these will be considered in a separate section. Others, such as a single tardigrade, a few specimens of the rotifer *Keratella hiemalis* Carlin, a single cladoceran *Bosmina* sp., and occasional specimens of the copepod *Cyclops scutifer* Sars (?), occurred mostly in the melt season, and were probably introduced to the lake from more stable freshwater habitats elsewhere. Others, including the cyclopoid copepod *Cyclopina* sp., and at least two species of harpactacoid copepods, are essentially epibenthic or littoral forms that appeared occasionally in very small numbers at the offshore sampling stations. Also in this category is the amphipod *Gammaracanthus loricatus* Sabine, which was noted in surface waters around ice and taken thrice in hauls through holes in the ice.

The other forms considered in this section are all considered to be permanent, holoplanktonic residents of the lake, but for various reasons are not given the detailed attention accorded above to the four large or abundant species.

Ptychocylis obtusa Brandt

Members of the tintinnid genus *Ptychocylis* were the only protozoans found abundantly in the samples. As they were about 70 × 100 μ, they were probably retained well by the fine-mesh nets. Most seem to belong to this species, with its blunt basal lobe, but they were somewaht variable in form. A number of other species of *Ptychocylis* have been described from northern waters, and have been given the status of "variety" or "forma" by some authors.

A few specimens were present at the begginning of the 1957 season in the inner and middle basins, but they disappeared, to reappear in mid-August in all basins. Peak populations were 300,000 per m^2 on August 31 in the outer basin, 230,000 per m^2 on August 17 in the inner basin, and 50,000 per m^2 on September 15 in the middle basin. Curiously, none were detected in the samples from 1962; possibly they occurred later in the season.

Their vertical distribution on August 21, 1957, was very restricted. Although they were probably undersampled by the medium-mesh net, 1720 per m^3 were taken near the surface at 3.1 m, 80 per m^3 at 5.7 m, and none in deeper hauls. The absence of the species in 1962 may therefore be related to the greater freshening near the surface of that year (McLaren, 1967b).

Although it attained high numbers, *P. obtusa* is very small, perhaps of the order of 0.001 μg C per individual (from extrapolation of the length-weight relation in Fig. 25 of similarly shaped *Aglantha digitale*). Unless its generation length was extremely short, it cannot have contributed significantly to secondary production in the water column; a stable population of 300,000 per m^2 undergoing fission would produce about 0.3 mg C per generation.

Melicertum octocostatum (M. Sars)

This hydromedusan has not apparently hitherto been recorded from the Canadian Arctic, although it is well known from brackish waters off Northern Europe and West Greenland. It was taken only once in the outer basin, but occurred sporadically in very small numbers through the 1957 season in the inner and middle basins. Mean numbers in 1957 (all sizes and all dates combined) were only 12 per m^2 in the middle basin and 7 per m^2 in the inner basin. It was rare in 1962: one was taken in the middle basin on June 29, and two more on August 10.

Unlike *Aglantha digitale*, *M. octocostatum* has a hydroid stage, and its life cycle in the plankton is not altogether clear. The largest specimens, three of which had ripening gonads, occurred at the end of the 1957 season, on September 15 and 29. Specimens taken in mid- and late August in the middle basin were small (2–3 mm in bell height), but one from the inner basin on August 31 was almost 6.5 mm; specimens from early June and early July were intermediate in size (3.5–4 mm). To the extent that these size classes are representative, they suggest that medusae may be produced in spring and generally mature in fall, a few overwintering to mature in spring.

The production of this species, similar in size to *A. digitale*, is not worth approximating.

Cyanaea capillata (L.)

This large scyphomedusan was seen commonly in the clear water at mid-depths, although postlarvae were not taken in the nets. A rough estimate of their abundance would be 0.01 per m^2, from observations in the summer of 1962. These ranged in diameter from a few to about 25 cm. Single ephyra (larvae) turned up in plankton hauls in the middle basin on September 15 and 29, 1957.

A large animal might weigh 5 g C (from length–carbon relationship of *A. digitale*, and consideration of shape differences). Assuming a mean abundance during life of 0.01 per m^2 (above) suggests a production of 50 mg per m^2 per generation. In view of the wide size range observed in summer, it is unlikely that this large form has an annual life history. A biennial life history would reduce the above estimate of production to the order of 25 mg C/m^2 per year, which is of small consequence compared with that of other predaceous zooplankters in the lake.

Ctenophores (*Beröe* sp.)

Ctenophore fragments were found in many samples, but were always beyond further identification. Apparently specimens were fragmented by the fresh water at the surface even before preservative was added. In 1962, ctenophores were conspicuous (spaced at horizontal intervals noted on one occasion as being somewhat more than 0.5 m) in a narrow stratum in the halocline, where they could easily be seen from the surface. They were apparently all *Beröe* sp., the largest about 3–4 cm long (much smaller than *Beröe* in the

sea). These full grown individuals might weigh about 20 mg C each (from extension of relationship for similarly shaped *A. digitale* in Fig. 25). Assuming an annual cycle and a mean density of 5 animals per m^2 (from spacing observations above), these populations could have produced 100 mg C/m^2 per year; this approximation, although very crude, suggests that the elusive ctenophores deserve more study as predators and producers in the lake.

Synchaeta tamara Smirnov

This rotifer is rather easily recognized as one of the few members of the genus with a single toe. It is known pelagically from the Barents Sea, and is therefore considered to be a true member of the saltwater plankton of Ogac Lake. It was noted in 1957 only in samples taken during August and September, but was more common during 1962 in July (Fig. 27). Curiously, it did not flourish in the fertilized column, and was not noted after the beginning of the

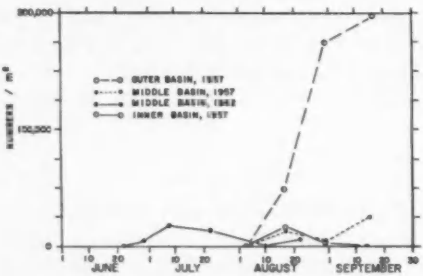


FIG. 27. Seasonal changes in abundance of the rotifer *Synchaeta tamara*.

experiment. The animal became abundant only in the outer basin, where, along with some 198,000 *S. tamara* per m^2, about 270,000 per m^2 of tiny, elongate eggs, believed to belong to this species, were found on September 14, 1957. Such eggs were otherwise noted only in very small numbers, and may have been undersampled, since their size (ca. 80 μ long) was near the mesh size (76 μ) of the fine nets.

Eleven specimens from the horizontal tows of August 21, 1957, were all at 7 and 9.8 m — that is, close to and within the temperature minimum. A few specimens on August 13, 1962, were taken by horizontal hauls at 6.8 and 12.4 m, but many more came from the colder water at 21.4, 23.8, and 26.6 m. This suggests a preference for cold water, which may be related to the greater abundance achieved by the species in the cold outer basin of the lake.

Production rates can only be guessed at. From comparisons with weight estimates for larval bivalves (see under section on Larvae of Benthos), which have a similar flattened ovoid form, it is thought that fully grown individuals of *S. tamara* weigh 0.1 μg C. The fact that eggs were abundant only in one sample suggests that reproduction was more nearly synchronous than continuous. It would be "generous" to assume that animals on each sampling

date represented separate, fully grown generations, but, on the other hand, assuming that no mortality occurs after the egg or very early stages would underestimate production. Together these assumptions lead to an estimate for production rates of 1 mg C/m² per day in the outer basin in early September 1957, and much smaller rates elsewhere and at other times. This figure implies that *S. tamara* contributes very little to the production of zooplankton in the lake.

The large differences in abundances between the three basins in 1957 and the differences in timing between 1957 and 1962 probably reflect the opportunistic character of *S. tamara*. Unlike other metazoan zooplankters of the lake, these rotifers probably can exist for long periods as resting eggs, and are able to increase rapidly when ecological conditions permit.

Eurytemora americana Williams

This estuarine or neritic species is known from Atlantic, Pacific, and arctic localities (Heron, 1964). It was taken in 1957 in all three basins, but only in mid-July and early and mid-August. Only a few specimens were taken in most of these samples, but the species acheived maxima on August 17 of 6200, 4500, and 1200 individuals per m² in the outer, middle, and inner basins respectively. These may be compared with some 275,000, 74,000, and 312,000 of the similarly sized *P. minutus* in the same basins on the same date. Clearly *E. americana* was not of much importance in the economy of the plankton in 1957.

In 1962 scattered individuals were found in samples in June and early July, but, as in 1957, the species only became common in August. In the middle basin, only a few were taken on August 10, but about 117,000 per m² were estimated on August 22. In the outer basin, about 31,000 per m² occurred on August 12 and 32,000 on August 22. These populations were fully one-quarter as great as those of *P. minutus* in the two basins on August 22.

The sudden appearance of *E. americana* in August of both years could not have been due to reproductive increments at the offshore sampling stations. In Tessiarsuk, a lake similar to Ogac Lake on the Labrador coast, the closely related *E. hirundoides* lives at the top of the halocline (Carter, 1965). The same seems true of *E. americana* in Ogac Lake. Only eight specimens were taken in the quantitative horizontal tows in the middle basin in 1957 and 1962, but seven were taken at the top of the halocline at 3.1–3.6 m. Samples taken just over *Fucus* beds near shore in July 1962 produced very large numbers of this species, as follows:

Locality and date	Depth (*m*)	Approx salinity (‰)	No. per m²
Outer basin, July 22	1.8	2	0
	2.5–3.0	5–17	4,500
	3.5–3.8	17.5	1,300
Middle basin, July 29	2.5	1	0
	3.0	10–15	59,600
	3.5	18	2,080

Clearly *E. americana* in Ogac Lake was not only a brackish form but also essentially epibenthic. Its appearance offshore in August represented a dispersion of these dense inshore populations. Its much greater abundance in 1962 may be related to the greater depth of the freshwater layer in that year (McLaren, 1967b). After the spring runoff, much of the sublittoral biota were dead, and the phytoplankton at the halocline was richer in summer (McLaren, 1969). The movement of surface waters that must have accompanied the greater freshening in 1962 would also have aided the offshore dispersion of *E. americana*.

The large samples from inshore and offshore in 1962 may be combined to show development of the species during summer (Fig. 28). It is assumed

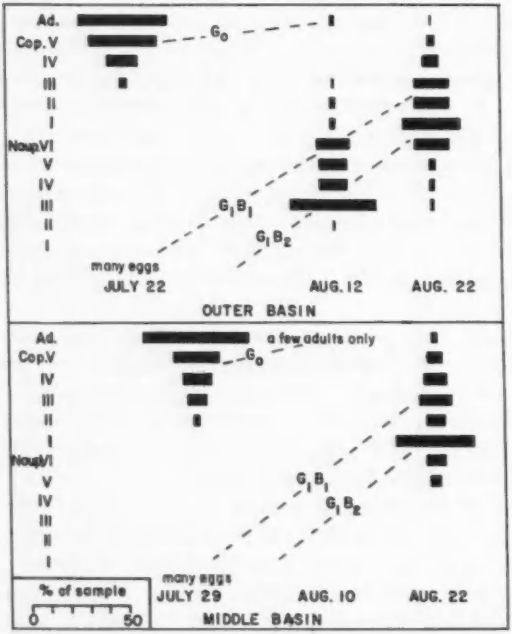


FIG. 28. Seasonal changes in proportionate numbers of stages of the copepod *Eurytemora americana* in 1962.

that the adults and older copepodites in July represented the overwintered generation (G_0). The distributions of stages in the offshore samples from August resembled those of *P. minutus* (Fig. 2), in having two distinct modes, assumed to represent the first (G_1B_2) and second (G_1B_2) broods of the new generation. The development rate implied in Fig. 27, from egg to stage III copepodite in less than a month, or about 0.3–0.4 stages per day, is very close to the maximal development rate shown by the similarly sized *P. minutus*. However, during late July and early August, development of *P. minutus* was almost stopped, whereas *E. americana* continued to grow by exploiting the rich food supply at the halocline, especially epibenthically.

Because *E. americana* appeared so irregularly in the offshore plankton, and achieved much of its growth elsewhere, it probably contributed little to production in the sampled water columns of the lake, especially in 1957. From abundance of the various stages offshore on August 22, 1962, and from weights of the similarly sized *P. minutus*, it is estimated that *E. americana* may have contributed some 85 mg C/m² to the middle basin. This figure assumes that all production occurred offshore, and ignores mortality prior to August 22; errors from the two assumptions may cancel out.

Calanus glacialis Jaschnov

In 1957 this species was taken in abundance in the outer basin only on August 31 and September 29, immediately after a series of tidal inflows. A few also occurred in the middle basin at these times, and five specimens were taken in the inner basin on September 29, which received quantities of tidal water for the first time in late September (McLaren, 1967b). These animals were probably allochthonous, and will be considered in a separate section.

The occurrence of a stage IV copepodite in the inner basin on June 6 and of another on August 3 suggest that a very tenuous population was resident in 1957. In 1962, small numbers (maximum 80 per m²) were taken in the middle basin on every sampling date between June 8 and August 10. An increase to some 600 copepodites per m² on August 22 could be attributed to tidal influx, but the earlier animals (mostly copepoidites IV and adult females) were certainly resident. Although no adults were taken in the fertilized column, spawning seemed to be successful, as a maximum of some 1760 nauplii per m² occurred on July 22, whereas only a few were taken in the middle basin.

Possibly the relative rarity of this species in the lake derives from the fact that, unlike the abundant *P. minutus* and *O. similis*, *C. glacialis* does not carry egg sacs. Much of its egg production in the lake may be lost to the anoxic depths before hatching.

The specimens of the putative resident *C. glacialis* were much smaller than the marine form. The adult females from the middle basin in 1962 averaged 3.35 ± 0.15 mm (cephalothorax length, and 95% f.l.), whereas those taken in tidal inflows were 3.60 ± 0.11 mm. The females from inflows were about average for arctic *C. glacialis*, whereas the lake specimens were as small as those from the Gulf of Maine (Grainger, 1963). Clearly the size differences are an ecophenotypic response to temperature.

A few adult females averaged 516 μg in dry weight, about 100 times as much as *P. minutus* in the lake. The resident population of *C. glacialis* in the middle basin was always less than 0.1% of that of *P. minutus* in 1962, and there was little evidence of spawning and no apparent development of "modes" of young. Therefore no attempt can be made to measure production rates, which were doubtless negligible. In the fertilized column, the young on July 22 (250 NV, 1510 NVI, and 165 CI per m²) probably gave rise to the older stages on August 9 (300 CIV and 100 CV per m²). If this is true, it implies a development rate of about 0.2 stages per day, about half the maximal rate

shown by *P. minutus*, but about the same rate shown by *P. minutus* in the fertilized column at the same time (Fig. 2). Assuming each stage of *C. glacialis* to be about 100 times as heavy as the equivalent stage of *P. minutus*, a net production rate of about 25 μg C/m^2 per day can be estimated for *C. glacialis* between July 22 and August 10, and perhaps about 1 mg for the season; this too is insignificant.

ECOLOGY OF PLANKTONIC LARVAE OF BENTHOS

Larvae of a number of benthonic species occur in the plankton of Ogac Lake. Since the fauna is restricted in diversity, the lake offers an opportunity for the precise matching of larvae with the adults. However, the benthos is largely as yet unanalysed, and only a few larvae have been identified to species.

All the larvae are here considered together under the headings of seasonal cycles, vertical distributions, and growth and production. Only the important forms are considered in any detail.

Seasonal Cycles

Two facts must be kept in mind in understanding seasonal changes in abundance of larvae in the water columns (Fig. 29, 30, 31): first, active or passive movement of larvae to the sampled water columns in the centers of basins must take place from aerobic bottoms nearer the shores; and second, the older larvae may begin to settle, perhaps to die in anaerobic water, while younger larvae are still being recruited from near-shore areas. For these reasons, samples from the centres of basins probably under-represent the overall numbers of larvae. This is even truer of the fertilized columns, which were cut off from any recruitment after they were set in the lake.

Bivalve larvae were in most samples (Fig. 29) the most abundant group. Only two bivalve species in the lake are known to have planktonic larvae. The larger specimens in the samples did not at all resemble the very distinct larva of *Hiatella arctica* (Thorson, 1946, fig. 182) and all or almost all are tentatively assigned to *Mya truncata* (Thorson, 1946, fig. 184). In all basins and in both years, there were modal classes of large larvae at the beginning of the season. These larvae were presumably spawned in the previous season and grew slowly and decreased in numbers during summer; they are designated by year of spawning (S-56 and S-61). Small larvae at the beginning of the season, some of which seemed to give rise to modal classes of intermediate-sized larvae in summer (S-57*a*, S-62*a*), were possibly another species; at any rate, the main period of recruitment of young larvae clearly occurred late in summer (S-57*b*, S-62*b*). This indicates that the larvae spent a full year in the plankton. Published information (e.g., Thorson, 1936) seems inadequate to determine if such a long life is characteristic of arctic bivalve larvae. The new mode (S-62*b*) in 1962 (absent, as expected, in the fertilized column) was much smaller than in 1957, but may not have been fully recruited by mid-August.

Various polychaete larvae (Fig. 30) were next in importance by virtue of their large size or abundance. These were classified into four stages: stage A

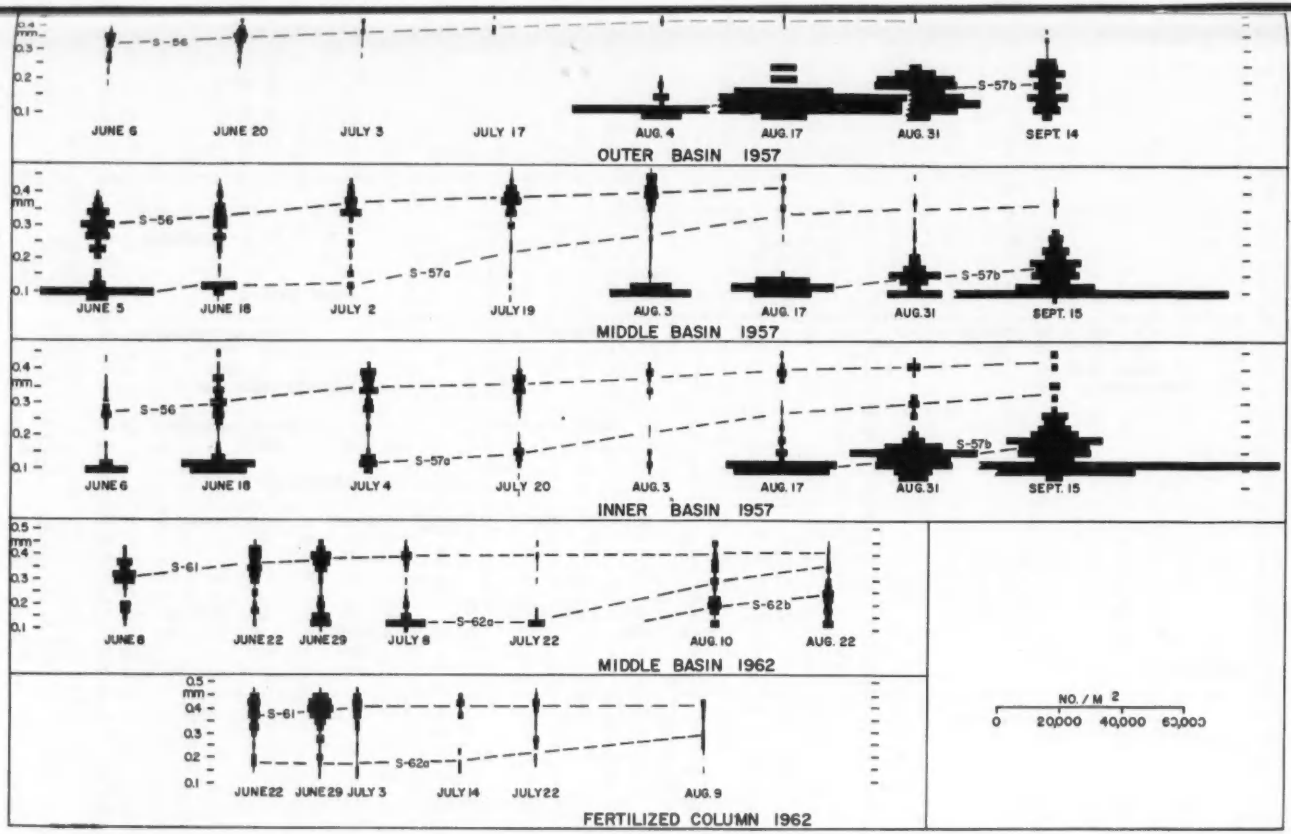


FIG. 29. Seasonal changes in size (length of shell) and number of bivalve larvae. The broken lines are designated according to the year of spawning (S-56, etc.) of the modal classes which they trace.

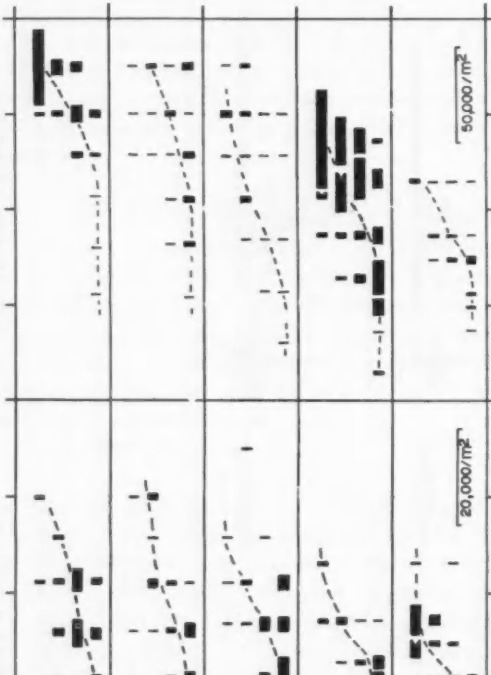


FIG. 30. Seasonal changes in numbers of polychaete larvae. The broken lines trace putative modal classes of development. A, B, C, and D are stages of development, as described in the text.

were larvae with no marked evidence of segmentation; stage B showed segmentation but little or no setation or limb development; stage C showed limb or setal development; stage D were old larvae, nearly ready to settle, with well-developed limbs or setal, and head parts. These stages conform roughly to eggs and early trochophores, early metatrochophores, and nechtochaeta respectively, as described by Thorson (1946). Assignment to stages was at times difficult, but Fig. 30 may be used as a general indication of differences between species, basins, and years.

The most generally abundant polychaete larvae (Fig. 30) were easily identified as *Cistenides* sp., and attributed to *C. granulata* as the only species recorded from the lake (Grainger, 1954). Recruitment occurred late in the season, and fully developed larvae were found mostly in late August and September. Few larvae occurred in the fertilized column, because of their late appearance in the lake.

Larvae attributable to the family Phyllodocidae were next in abundance (Fig. 30). It is possible that more than one species was involved, as young stages could not be separated with certainty. These appeared early, and were therefore well represented in the fertilized column, where they seemed to suffer little mortality during development. Development was much slower and mortality higher in the lake waters than in the fertilized column.

Very large polychaete larvae, apparently belonging to a single species of the family Polynoidae were well represented (Fig. 30). Young specimens (stage A) predominated early in the season, although a second maximum of stage A occurred later in the middle basin in 1957. Most fully developed specimens (stage D) did not appear until summer; those in the inner and middle basins in June 1957 seem clearly to have overwintered from the previous season. The large larvae of this species may therefore spend a year in the plankton when conditions demand it.

Other polychaete larvae, among which were species of the families Glyceridae and Spionidae, were not as common (Fig. 31.) Numbers of gastropod and echinoderm larvae, of several species and sizes, are combined on Fig. 31. A few nauplii of *Balanus*, presumably *B. balanoides*, were found mostly early in the season, and some cypris larvae were taken beginning in early July (Fig. 31).

A few comments can be made about the differences between the various basins and years (Fig. 29, 30, 31). Generally, the largest concentrations of larvae occurred in the outer basin, which is to be expected as the small size of the basin afforded easy transport of larvae from nearby shallow areas. Most kinds of larvae were much more common in the middle basin in 1962 than in 1957 (Fig. 30, 31). It is unlikely that the difference was due to much greater larval production in 1962. The offshore abundance of the littoral copepod *Eurytemora americana* in 1962 has been attributed to greater water movement near the surface that year (see above, under this species). Only older larvae tended to migrate at night into shallower waters (see below), which might have made them more subject to such horizontal transport. The *apparently*

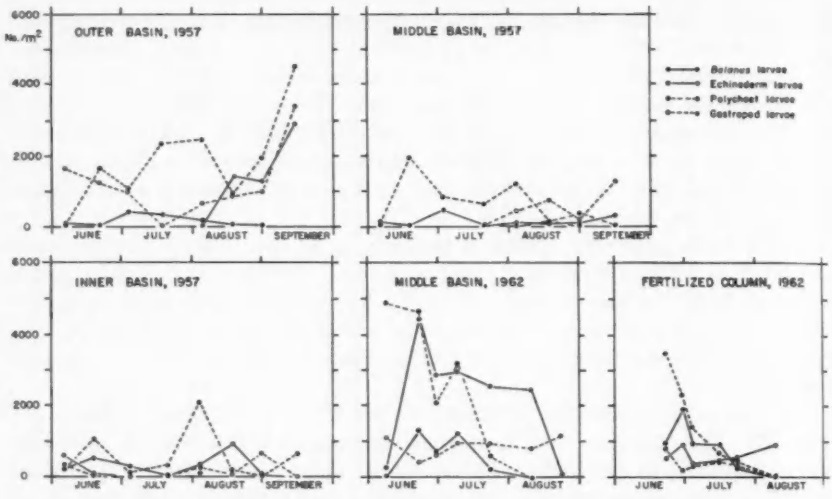


FIG. 31. Seasonal changes in abundances of less common larvae.

faster development of some polychaetes in 1962 than in 1957 (Fig. 30) may be attributable to such selective transport of older larvae to the offshore sampling sites, rather than to better conditions for the growth of larvae in 1962.

VERTICAL DISTRIBUTIONS

Only those larval forms that were sufficiently common were studied for vertical distributions (Fig. 32).

Little can be said about the distributions under the ice on July 8, 1962, except that, like the copepods in the lake, larvae were generally most common at mid-depths. Larvae of *B. balanoides* (not shown on Fig. 32) were most common at 15–20 m.

In the two daytime collections from August, most larvae were likewise at mid-depths, but there were differences between species and between years. For example, on August 8, 1957, the large polynoids were concentrated at the temperature minimum (cf. Fig. 5) at 10 m, whereas the bivalve larvae were commonest in warmer water above and below that depth. In 1962, when no such temperature anomalies were present, the two larval forms showed similar distributions.

In contrast to the holoplanktonic species discussed earlier, all the larvae, except possibly *C. granulata*, displayed migratory tendencies. Careful reference to Fig. 32 shows that the apparent shifts in maxima cannot be attributed to differences in depths sampled by day and night. Among the forms in which stages of development were distinguished, the older larvae were more clearly m gratory.

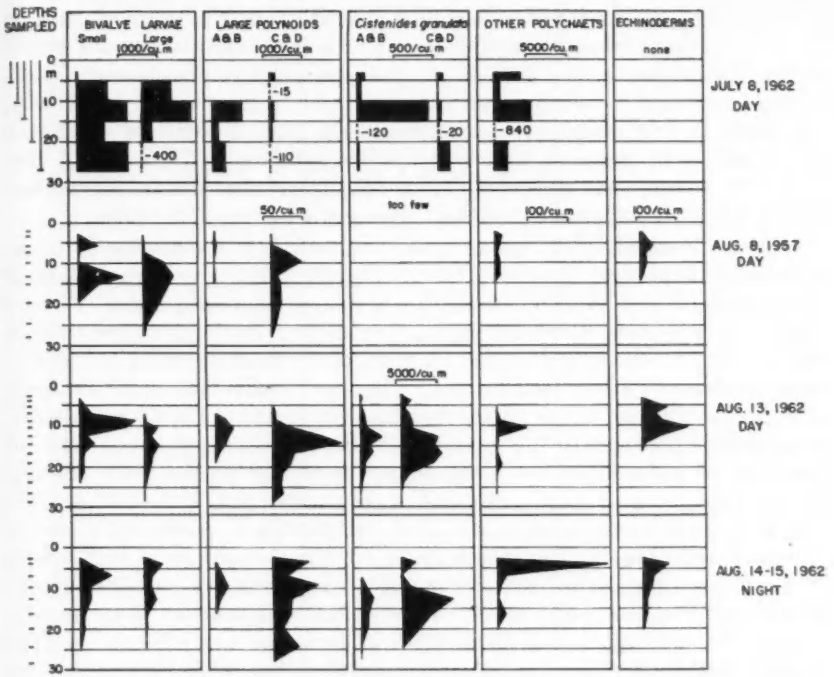


FIG. 32. Vertical distributions of the most abundant larvae in the middle basin on four occasions. A and B are young stages and C and D are later stages of the two polychaete species (see text).

GROWTH AND PRODUCTION

Because of the large numbers of species, the relative scarcity of many, and the fact that samples from the middle of the basins were not representative (see above), it was not possible to make detailed calculations of production of benthonic larvae between sampling dates. However, a number of approximations were used to estimate production on a seasonal or annual basis.

A preserved sample of 50 bivalve larvae, all of about the same size, averaged 0.38 mm long and contained 1.3 μg C per individual. Carbon contents of other size classes were estimated by assuming a cubic length–weight relationship. The modal classes of bivalve larvae on Fig. 9 are particularly clear, but could not be used directly. (1) The largest individuals of S-56 and S-61 presumably settled or died more rapidly than small individuals during summer, which would lead to an underestimate of production. As an approximation, it was assumed that, before disappearing, individuals reached lengths represented by the length distributions of these modal classes (S-56 and S-61) in samples from August, and that the total numbers achieving this size were equal to the mean numbers present in the two groups in June. (2) The main new modes (S-57*b*, S-62*b*) were not fully represented in the samples until they had gained

some growth. It was therefore assumed that the initial number of spawned larvae was equal to the largest number present in the modal class during August or September (easily seen in Fig. 19). (3) The small summer modes (S-57*a*, S-62*a*) were used to calculate production in the usual manner. (4) Finally, the last and first samples in each basin were used to estimate production during winter by assuming that S-56 was derived from S-57*b*, and S-61 from S-62*b*. These combined estimates (Table 10) suggest that bivalve larvae were among the most important producers among the larvae of the lake.

Simply integrating changes in sizes and numbers in the developing modes of the more important polychaete larvae (Fig. 30) would give low estimates of production, because of unrepresentative sampling mentioned above. For this reason, use was made of approximations that might actually give more accurate results. (1) All estimates of carbon contents of the large polynoid larvae were based on determinations for 60 stage A (2.2 μg C/individual) and 50 stage D (4.8 μg C/individual) larvae. Values for the other larvae in Fig. 30 were derived by applying for all species the same relationship between carbon contents and estimates of volumes of the larva stages as applied to the large polynoid larvae. Thus, stage A were taken as 0.4 μg C and stage D as 1.2 μg C for the phyllodocid larvae, and as 0.3 μg C and 1.0 μg C respectively for the *C. granulata* larvae. (2) The largest single population estimate of each species in the five seasonal series of tows in Fig. 30 was used as a measure of mean abundance. The bias produced by this procedure was assumed to be counterbalanced by the lag in full recruitment of larvae at the offshore sampling stations, and by the later settlement or death of the older larvae. (3) This estimate of mean abundance was then simply multiplied by the difference in weight between stage A (assumed to be the same weight as eggs) and stage D larvae. This approach, although very crude, approximates production for the year, whether highly seasonal or extended through the winter (Table 10).

Finally, the remaining less common larvae (Fig. 31), for which development stages were not consistently separated, were treated similarly to the above polychaete larvae. (1) From size measurements and comparisons with similarly shaped forms whose carbon contents were known, the weight increments between eggs and settlement stages were taken as 3.0, 0.2, 0.2, and 0.1 μg C for larvae of barnacles, "other" polychaets, echinoderms, and gastropods respectively. (2) These increments were multiplied by the *maximum* counts of each larval form in the sample series. Production by these less common larvae was very small (Table 10).

Although many approximations have been used in calculating production by larvae, the errors may tend to cancel out. The total estimates in Table 10, except for the fertilized column, which was cut off from larval recruitment in summer, are similar. Compared with the copepods, the larvae contributed little to secondary production: the combined totals in Table 10 are only about 13% of the combined totals of production by *P. minutus* and *O. similis*.

TABLE 10. Estimates of annual net production of larvae of benthos in Ogac Lake, in mg/m³ per year (per season in fertilized column).

Basin and year	Bivalve larvae	Large polynoid larvae	Phyllodocid larvae	*Cistenides granulata* larvae	Other polychaete larvae	Barnacle larvae	Echinoderm larvae	Gastropod larvae	Total
Outer 1957	51.0	6.1	6.3	32.3	0.9	1.3	0.6	0.3	98.0
Middle 1957	62.0	4.8	3.5	4.1	0.4	1.3	0.1	0.1	76.3
Inner 1957	50.5	7.8	4.5	4.1	0.5	1.7	0.1	0.1	69.3
Middle 1962	22.4	14.0	4.2	58.8	1.0	4.1	0.3	0.1	104.9
Fertilized column 1962	8.8	3.8	4.0	2.8	0.6	5.9	0.2	0.1	26.2

ECOLOGY OF ALLOCHTHONOUS ZOOPLANKTON

Quantities of Zooplankton Entering the Lake

The tides bring large quantities of zooplankton into the lake from the sea (Table 11). The amount and quality must vary with time of day and weather conditions, as well as seasonally, but the plankton was sampled only once or twice during each series of tidal inflows in 1957 and 1962, by techniques described in Materials and General Methods.

Smaller organisms (small copepod species, nauplii, benthonic larvae, etc.) are not listed in Table 11 because they largely passed through the meshes of the nets used in 1957. For the same reason, younger copepodites of *P. minutus* were undersampled, and estimates for this species in Table 11 are too low. However, the larger forms made up the bulk of zooplankton entering the lake, and estimates of biomass (from dried subsamples) are probably only slightly too low.

The greatest amount of zooplankton entered in summer (Table 11). Earlier in the year the surface waters of the sea near Ogac Lake are somewhat brackish, and probably avoided by many species. Swarms of epibenthic and littoral forms (mysids and amphipods) are also swept into the lake in summer; this swarming activity may diminish in autumn.

An estimate can be made of the total biomass entering the lake in 1957. It is assumed that samples in Table 11 are representative of their respective series of tidal inflows in 1957, except that of August 26, for which the more complete estimate of August 17–18, 1962, is substituted. The biomass for September 24 is assumed also to apply to the unwitnessed tides of late October. The amounts of water entering the lake are given by McLaren (1967b, table III). From these it is calculated that about 1200 kg dry weight of zooplankton entered the lake in 1957. This estimate is probably somewhat low.

Fate of the Allochthonous Forms

The incoming organisms seemed largely ill-adapted to the waters of Ogac Lake. Young fish (mostly cottids), mysids, and amphipods (mostly *Gammarus setosus*, *Themisto libellula*, and *Pseudalibrotus* spp.) fall prey to the voracious codfish (Patriquin, 1968) that school in the lake near the outlet at high tides; these animals were never taken in plankton samples from the lake. Others, like ctenophores and medusae were also eaten by codfish, but were sometimes found dead or in fragments in samples from the outer basin of the lake; they may have suffered from the lowered salinity and the great turbulence of the inflows.

Calanus glacialis was sometimes the most abundant species in the inflows (Table 11). Copepodites of this species were well sampled by the nets of no. –6 mesh, and an estimate of the numbers entering the lake can be made for each series of tidal inflows from Table 11 and from McLaren (1967b, table III). The numbers in the outer basin, which retains almost all the tidal water

TABLE 11. Numbers and biomasses of various zooplankton per m^3 in representative tides of each series of inflows entering Ogac Lake. The values are means where more than one tide was sampled in each series.

Date	Vol of inflow ($m^3 \times 10^6$)	Medusae and ctenophores	*Limacina helicina*	*P. minutus* copepodites	*C. glacialis* copepodites	Amphipods	Mysids and decapods	Young fish	Biomass dry wt (mg/m^3)
1957									
July 1 PM	167	0.07		94		0.48	2.49	0.08	4
30 PM	96								
July 28 PM	233			143	497	2.90	10.40	0.30	44
30 AM	148								
Aug. 26 PM	326	0.02		6[a]	11[a]	2.86	29.90	1.54	137+
Sept. 24 PM	348	0.07		2640	237	5.39	0.13	0.07	49
1962									
July 20 PM	84	2.56	4.95	4	32	1.65	2.54	0.15	76
Aug. 17 PM	278			423	1930	1.09	4.90	1.09	387
18 AM	198								

[a]The no. 6 net sample was lost, and the copepods greatly undersampled.

can be approximated from area of the basin and numbers per m^2, as determined in the standard plankton series. The numbers, in millions of individuals, are as follows:

Tidal series	No. entered	No. after tides	No. ca. 2 weeks later
1957			
Late June	0	0	0
Late July	580	50	4
Late Aug.	Not estimated	260	2
Late Sept.	510	60	Not observed
1962			
Mid-Aug.	3200	1090	Not observed

Although these figures can only be taken as gross approximations, they show clearly that *C. glacialis* is subjected to great mortality in the lake, and that few survive for more than a week or two. Nevertheless, there appears to be a small resident population of this species in the lake (see above) and some may survive from the inflows.

The few *C. glacialis* that survived 2 weeks in the outer basin did not average significantly smaller than those in the tidal inflows, although they averaged significantly larger than resident copepodites from the middle basin in 1962.

Pseudocalanus minutus was abundant in most tidal inflows (Table 11). There was no overlap in size between copepodites from the lake and those from the sea or the tidal inflows. The large form of *Pseudocalanus* (Woods, 1969), was very rare or absent in the outer basin in 1957 and 1962. Thus allochthonous *P. minutus* could easily be distinguished there. Only once, among stage I copepodites at the end of September, was there the slightest "contact" between the two size groups. The numbers of allochthonous copepodites in the outer basin immediately after each series of tidal inflows in 1957 usually exceeded the numbers predicted from inflow samples, because the incoming *P. minutus* were much undersampled by the nets (see above). The species was more accurately sampled in mid-August 1962. About 700 million copepodites occurred in the 1.6 million m^3 of water that flowed into the lake. On August 22, 1 day after the last inflow, there were about 1090 of the large allochthonous copepodites per m^2 in the outer basin. This suggests a total population there of the order of 200 million, again implying large mortality. Two weeks after each of the tidal inflows in 1957, very few allochthonous copepodites remained in the outer basin, as the following comparisons (in no. per m^2) show:

Tidal series of inflows	No. immediately after series	No. 2 weeks later
Late June	3,170	300
Late July	12,440	270
Late Aug.	830	220

The very high mortality of the allochthonous copepods is the counterpart of the mortality apparently inflicted on the resident *P. minutus* by the tidal inflows (see above under Life Cycle and Population Dynamics of *P. minutus*). Again, it is impossible to be certain of the cause of mortality, but sharp changes in temperature and perhaps salinity may be suspected.

Allochthonous *P. minutus* were not only greatly reduced in numbers, but the few remaining were also much smaller after 2 weeks in the lake. Figure 33 depicts sizes of the few putative allochthonous copepodites that occurred in the outer basin 2 weeks after the tides. These are compared with size distributions in the inflows (or in the sea, where the inflow sample of late August was not adequate), and in the lake immediately after the series of tidal inflows. Although the recognition of some allochthonous individuals might be disputed (the division between allochthonous and resident forms of *P. minutus* on September 14 is arbitrary), all the data in Fig. 33 taken together give strong evidence that some individuals from the sea survived and molted to a smaller size in the warmer waters of the lake. It is possible that a few individuals molted a sufficient number of times to become indistinguishable from the equivalent indigenous stages. Some might mature and breed with the lake population, and these, together with allochthonous females that carry viable eggs when they enter the lake, may maintain a small amount of gene flow between the *P. minutus* of the lake and the sea.

In conclusion, it seems clear that the zooplankton from the sea contributed almost nothing to the faunal composition of the lake. The tidal population does offer general organic enrichment. This enrichment may be especially important, since inflowing waters are depleted of nutrients and are very low in chlorophyll, and presumably phytoplankton (McLaren, 1967b). In fact, the total biomass of inflow organisms (1200 kg dry weight) was about equal to half the total zooplankton production in the lake in 1957 (ca. 1500 kg in carbon, and perhaps twice this in dry weight).

DISCUSSION

General Ecological Characteristics of the Zooplankton

The species in Ogac Lake are a selection of widespread marine forms. There appear to be no "relict" zooplankton species (like the resident codfish *Gadus morhua*), with the possible exception of the medusa *Melicertum octocostatum*, which may be boreal in distribution. Some other common arctic species may be absent or rare because of special deficiencies in the lake (see, for example, the suggestion that free eggs of *Calanus glacialis* may be lost in the anaerobic depths). It is also possible that intensified competitive interactions exclude some species. Certainly the common copepods of the lake occupy very different niches: *Pseudocalanus minutus* and *Oithana similis* exploit different seasons, depths, and probably food supplies, and the littoral *Eurytemora americana* was an opportunist in the near-surface layers in 1962. Similarly, the predators differed from one another markedly in depth distributions and

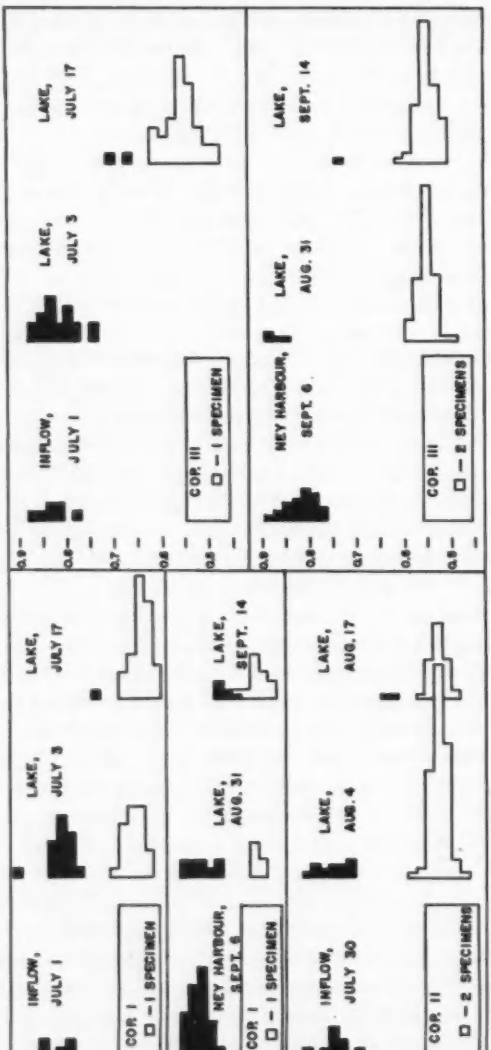


FIG. 33. Size-frequency distributions of copepodites of *Pseudocalanus minutus* in the outer basin of Ogac Lake, in the sea outside, and in inflows into the lake. Allochthonous individuals in black (see text). The stages involved and the scales are given for each panel.

seasonal cycles; it is possible that the extreme scarcity of adult *Aglantha digitale* in the shallow outer basin at the end of winter in 1957, and the numerically small generations that followed, were due to forced coexistence of this species with *Sagitta elegans*, which can occupy deeper strata in the other two basins. Such clear niche diversification may be characteristic of lakes in general

(Rigler and Langford, 1967) and landlocked fiords in particular (Carter, 1965), but may be absent or obscure in the sea at large.

Life Cycles and Population Dynamics

In spite of the quantitative detail presented in this paper, population dynamics of the zooplankton are in many ways obscure. One generalization seems evident: the controls of population growth and size may be largely "intrinsic," in the sense of being independent of amounts of food. Thus the reproductive rates and subsequent numbers in broods of the copepods in Ogac Lake are determined by the numbers and body sizes of the females during the short periods of abundant food supply, and the numbers in populations of *S. elegans* in summer are clearly determined by numbers of adults present at the time of recruitment, and unaffected by amounts of food prevailing then.

There has been much pre-occupation with food and feeding rates in studies of zooplankton. Laboratory populations, such as those studied by Slobodkin (1954) have indeed demonstrated a satisfying proportionality between food supply and standing crops. But it must be remembered that such studies are intended to reveal equilibrium situations (although intrinsic fluctuations may be involved). In highly seasonal natural environments, characteristic of middle and high latitudes, the important determinants of population dynamics may occur at times when food is greatly in excess of the ability of zooplankton to consume it. For these reasons, I feel that more study of the physiological limits of development rate, fecundity, and egg production rate, especially as influenced by temperature (McLaren, 1965, 1966a; Corkett and McLaren, 1969), will be more revealing of factors controlling zooplankton populations than will enquiries into food and feeding relations.

It is of related interest to note the general retention of an annual life cycle in the lake (*A. digitale* is a clear exception), in spite of mean annual temperatures that are closer to those of temperate seas than to those of the arctic. The long life cycles in high latitudes are not a direct imposition of low temperatures, but an adaptation to the restricted seasons of production. There appear to be two different approaches to ensuring the "correct" seasonality. The first is exemplified by *P. minutus*, which produces a series of viable broods when food is abundant, the earlier of which may mature and spawn in late summer and become "wasted," and the later of which may develop to a stage suitable for overwintering. The second is shown by *S. elegans*, in which adults may mature, spawn, and die before and after the period when food is adequate for their young, but in which the successful recruits suspend development during summer to mature in the following spring. These two strategies may be related to the degree of similarity of diet of adults and young; adult *P. minutus* may produce their eggs using the same phytoplankton food that satisfies their nauplii, whereas adult *S. elegans* may not be able to use or even detect the small prey used by their young, and may have to depend on general seasonal indicators.

Vertical Distribution

Two practical conclusions arise from the detailed studies of vertical distribution in this paper. First, even by using closely spaced depth intervals in sampling, maxima or minima of numbers of organisms can be missed (see comments on unsampled depths in the night hauls under the various species). Numerous published studies on vertical distribution or migration of zooplankton may be misleading since they are based on much more widely spaced sampling, although not as a rule in environments as strongly stratified as Ogac Lake. Secondly, differences between developmental stages of a species may be just as great as differences between species; it is not possible to generalize about diurnal, seasonal, or geographical differences in depth of a species from studies of all stages combined or of a single stage, although there are many such studies in the literature.

The observations from Ogac Lake reveal little of the proximate or physiological aspects of vertical distribution and migration, although certain relationships to salinity, temperature, and food supply are evident in the text. Support is partial and indirect at best for the arguments by McLaren (1963) on the adaptive value of vertical migration as a device for controlling growth and development, and maximizing rate of increase. The fact that diurnal vertical migration was not strongly evident among the holoplanktonic forms, except young *S. elegans*, is in agreement with other observations from arctic regions. McLaren (1963) suggested the low temperatures and limited stratification generally found in high latitudes would negate the adaptive value of vertical migration; some species in Ogac Lake may not be genetically adapted to take advantage of the warm, stratified waters there. A number of species in the lake showed ontogenetic descent from near the warm surface to the cooler depths, which can be understood as an adaptation for rapid growth of the young and, after the season of high production, for reduced development rate and metabolism of the older stages. The behavior of *P. minutus* in the temperature minimum in 1957 (see under that species) certainly suggests that the adaptive value of ontogenetic descent lies in low temperatures rather than deep water. The lack of a clear relationship between temperature and vertical distribution of *O. similis* is in keeping with the limited effect of temperature on size of this species (see also discussion of *O. similis* in McLaren, 1963). However, the similar lack of relationship between temperature and vertical distribution of *A. digitale* is accompanied by a profound effect of temperature on size of this species. Finally, the older larvae of benthos are more strongly migratory than the holoplanktonic species in the lake. Although the migration of larvae through temperature gradients may have marked effects on their growth and development, its adaptive value cannot be understood in terms of fecundity and maturation rates considered paramount by McLaren (1963).

The problems of vertical distribution and migration in Ogac Lake have only been studied to a limited extent. Clearly further studies of individual species through the season in such highly stratified waters may reveal much about the mechanism and adaptive values of vertical migration.

Growth and Development

The results of studies of Ogac Lake support laboratory and field evidence (McLaren, 1965, 1966b) of the over-riding influence of temperature in determining body size of a wide variety of zooplankton. The complexity of interpretation required to understand seasonal changes in size of *P. minutus* in Ogac Lake may seem inelegant, but any simpler approach would be naive. In my opinion, attempts to determine effects of food and temperature on size of zooplankters using regression analysis of seasonal collections (e.g., Deevey, 1964; El-Magharaby, 1965; Stone, 1966) may be inadequate without detailed knowledge of life histories and the actual temperatures experienced by the developing organisms, and recognition that temperature and food supply are often dependent variables. I believe that food has only or mainly an indirect effect on size of many zooplankters by determining the times when growth and development take place.

Related problems occur in the study of growth rates of zooplankton in nature. As the studies on growth increments of copepods have shown (see under *P. minutus* and *O. similis*), growth rates, development rates, and mortality rates may be intimately linked in individuals in ways that make interpretation from populations difficult. These problems, which have occupied the attention of fisheries biologists, have not been adequately considered by planktonologists.

Production

Total zooplankton production was of the order of 1 g/m² per year for the lake as a whole (Table 12). Not included are the crude estimates of production by *Cyanaea capillata* and ctenophores of about 100 mg/m² per year; these may at least in part represent the highest trophic level in the plankton. No comparable calculations for total zooplankton production in other marine or freshwater habitats seem to be available in the literature. However, it is clear that zooplankton production in Ogac Lake is quite small; mean annual standing crops of zooplankton were of the order of 400 mg/m² per year, similar to those of the Sargasso Sea (Beers, 1966).

Primary production in the middle basin during the summer of 1962 was about 9 g/m² (McLaren, 1969). "Herbivore" production (*P. minutus*, *O. similis*, larvae, and "others" in Table 12) during the same period was about 650 mg/m², which seems in agreement with various existing measures of ecological efficiencies. However, in spite of greatly increased primary production of about 60 g/m² in the fertilized column experiment (McLaren, 1969), secondary production was only about 900 mg/m².

Annual carnivore production (*A. digitale*, *S. elegans*) ranged from 16 to 36% of secondary production in the three basins in 1957; the estimate of 68% in 1962 seems very high.

Annual production/biomass ratios (P/B) for the zooplankton as a whole (excluding "others") ranged from 2.4 to 3.3. Ratios for individual species were rather variable (Table 12), but showed some patterns. For example,

TABLE 12. Estimates of net production (mg/m³) and production/biomass ratios (in parentheses after production estimates) for Ogac Lake zooplankton. Values are annual for the lake and for the period between June 22 and August 9 for the fertilized column. The P/B ratios are derived from integration of curves from seasonal samples, and the same assumptions used to estimate overwinter production (see under production of each species or group in the text) were used to estimate mean standing crops during winter. Production of *S. elegans* in the fertilized column could not be estimated because of sampling errors, and production of "other" zooplankton was very small except in the middle basin in 1962.

Species or group	Outer basin 1957	Middle basin 1957	Inner basin 1957	Middle basin 1962	Fertilized column 1962
Pseudocalanus minutus	410(8.3)	511(7.1)	354(4.9)	442(4.0)	712(3.4)
Oithona similis	347(3.0)	202(2.3)	223(3.5)	223(4.2)	92(2.6)
Sagitta elegans	196(2.1)	62(1.7)	49(1.9)	318(1.0)	Not estimated
Aglantha digitale	13(9.0)	193(10.2)	57(3.4)	263(3.5)	32(4.7)
Larvae of benthos	99(1.8)	76(2.2)	70(3.2)	105(1.2)	26(0.7)
"Others"	Not estimated	Not estimated	Not estimated	85*	Not estimated
Total	1065(3.1)	1043(3.2)	753(3.1)	1436(2.4)	862+(3.0)

*P/B ratio not estimated.

they were low for the larvae of benthos, which may depend largely on food stored in the egg, and were higher for *A. digitale*, which has two generations per season, than for *S. elegans*, which is annual in the lake. Although P/B ratios may prove widely applicable (Mann, 1969), they cannot be assumed to be strictly "physiological" and determinate; for example, the high ratio for *P. minutus* in the outer basin in 1957 seems to be traceable to the mass mortality of the copepods due to tidal influx (see under Life Cycle and Populations Dynamics of this species), which eliminated the large standing crop *after* much of its production had been achieved.

The estimates for Ogac Lake show clearly that zooplankton production cannot be measured or "explained" without detailed quantitative studies of life histories. This may be generally true in highly seasonal environments, where growth rates and reproductive rates are "intrinsically" determined during periods of high food supply. The fertilization experiment stresses this conclusion, since increasing the magnitude of phytoplankton crops without increasing the duration of the period of high phytoplankton availability had little or no effect on zooplankton production.

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Primary Production and Nutrients in Ogac Lake, a Landlocked Fiord on Baffin Island[1]

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Primary production was about 12 g/m^2 in the middle basin of Ogac Lake during 1962. Production was limited by available N, probably largely by amount of nitrate available at the end of winter. Production was largely concentrated in narrow strata — one descending from near the surface in June to occupy nutrient-rich deep water in summer, and another developing at the halocline in summer, possibly sustained by nutrients from freshwater kill of the littoral biota in 1962.

Polyethylene columns, 1 m in diameter and 30.5 m long, were set between the fresh surface and anoxic depth of the middle basin in 1962. A four-fold increase of nitrate and a two and a half-fold increase of phosphate led to a parallel uptake of the two nutrients in the columns, and to an approximately five-fold increase in mean amount of chlorophyll and a seven-fold increase in primary production compared with the lake during the period of the fertilization experiment.

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INTRODUCTION

THE PRIMARY AIM OF THIS STUDY is to supply background information for the more extensive work on zooplankton carried out at Ogac Lake (McLaren, 1969). The general character of the lake and its physical and chemical properties have been described elsewhere (McLaren, 1967a, b). Most of the field work was done in the summer of 1962, but limited data are available from 1957 for comparative purposes.

The work is incomplete, but the environment is rather unusual, and perhaps worthy of study as such, and is especially suitable for the study of certain general problems in primary production and nutrient dynamics. Ogac Lake is strongly stratified (meromictic) and almost cut off from the sea, so that events in the water column can be followed without complications from vertical and horizontal exchange. Experiments in fertilized polyethylene columns, like those described in this paper, can easily be carried out because of the protected setting and vertical stability of the lake. I hope that the limited observations in this paper might encourage others to carry out more detailed and revealing studies in Ogac Lake and similar environments.

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[1]The sixth paper in a series of studies on Ogac Lake.

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MATERIALS AND METHODS

All depths given are corrected to the same datum (surface at low lake level in early August 1962) so that seasonal changes in the water columns could be assessed more exactly.

Chlorophyll, oxygen, phosphate, nitrate, and nitrite were measured according to techniques given in McLaren (1967b).

Measurements of ^{14}C uptake were made using 125-cc glass-stoppered bottles. The ampoules with radiocarbon (1 cc, 4 μc) were supplied by the International Agency for ^{14}C Determination, Charlottenlund, Denmark, who also supplied the filtration apparatus and membrane filters, determined counts, and calculated production from data on total carbon. The recent upward correction of all counts made by this agency (Goldman, 1968) has not been applied to measurements from Ogac Lake, and it is probable that all estimates of primary production given here should be increased by about 45%. The bottles were suspended at the depths from which the samples were taken, for 24 hr, beginning around midday. The bottles were kept in a dark, snow-filled box when removed from the water, and the contents usually filtered within ½ hr. Dark bottles were not always used at all depths in deeper waters, so corrections were interpolated where necessary from dark-bottle uptake at adjacent depths. Unfortunately, because of instrument difficulties, calculations of total CO_2 (McLaren, 1967b) were made only on August 25, 1962. In order to estimate CO_2 values for calculation of ^{14}C uptake on earlier dates, it was assumed that all changes in CO_2 were biogenic, and related to seasonal changes in oxygen content by photosynthetic and respiratory coefficients of unity. This was unlikely to be valid near the surface, where freshening led to low CO_2 values late in the season. Therefore, waters above 5 m having the same salinities were assumed to have the same CO_2 contents. The amplitudes of seasonal change implied by these crude approaches were generally less than 10% of the CO_2 contents on August 25, and therefore the resulting errors are probably small compared with errors from other sources. No effort has been made to correct rates of production from estimates of incident light, which were made only irregularly during the season. Except for the experiments of June 25–26, July 3–4, and July 5–6, which were on almost cloudless days, experiments were performed in more-or-less "average" weather conditions, with the sun obscured one day and not the other, or with variable cloudiness throughout.

In 1962, large polyethylene columns (Goldman, 1962) were anchored and suspended in the middle basin of the lake between the anoxic depths and the fresh surface layer. These columns were made of sheets 100 ft long and 10 ft wide, and were therefore about 30.5 m long and 1 m in diameter when completed.

Four of these columns were lowered rapidly through holes in the ice of the lake on June 20, and known amounts of both nutrients (as KNO_3 and KH_2PO_4) were distributed throughout two of the columns by a garden hose as outlined by Goldman (1962). Although the hose was kept in the columns for a few minutes before withdrawal to allow thermal equilibration of its contents, the solutions were made up of water from mid-depths and could not be equilibrated to the marked salinity gradient of the lake. The first of the fertilized columns was sampled regularly for chlorophyll, oxygen, nutrients, and zooplankton until it sank accidentally in early July. Thereafter samples were taken from the second identically fertilized column, which became open along its seam after August 10 and sank soon after.

Fertilization was intended to raise concentrations of nutrients in the shallower waters to about 2.5 and 25 mg-at/m^3 PO_4–P and NO_3–N respectively, which required addition of 1.7 and 20 mg-at/m^3 to the columns. The actual concentrations observed in the column shortly after fertilization on June 20 departed quite widely from the theoretical amounts calculated from concentrations in the lake on this date (Table 1). This was clearly due to local concentrations of the added nutrients, which apparently became more evenly distributed by June 28 (Table 1, see especially changes at 11.7 m, as nutrient had become depleted in shallower water). Therefore, for the purpose of following nutrient uptake at each depth in the columns, theoretical rather than observed concentrations are assumed for the initial sampling date on June 20.

One unfertilized "control" column was sampled in early July and again in early August. Comparisions with the lake (Fig. 1) suggest that the polyethylene column had little effect on

TABLE 1. Concentration of nutrients observed in the fertilized column and theoretical concentrations expected from addition of 1.7 mg-at PO_4–P/m^3 and 20 mg-at NO_3–N/m^3 to amounts observed in the lake on June 20 and June 28.

	PO_4–P (*mg-at/m³*)			NO_3–N (*mg-at/m³*)		
Depth (*m*)	Theoretical June 20	Observed June 20	Observed June 28	Theoretical June 20	Observed June 20	Observed June 28
2.6	2.09	2.38	1.02	20.4	37.2	9.3
4.0	2.09	2.21	.89	20.5	23.9	3.5
5.9	2.30	3.05	1.23	20.3	41.3	6.3
7.8	2.39	3.14	1.71	22.8	34.4	11.0
9.8	2.51	2.35	2.12	24.0	27.1	19.3
11.7	2.55	4.67	2.49	25.3	59.6	24.3
14.6	2.62	2.61	2.54	24.9	26.4	25.4
19.4	3.02	2.64	2.97	24.6	23.3	23.5
24.3	3.86	3.78	3.85	29.3	32.1	28.7

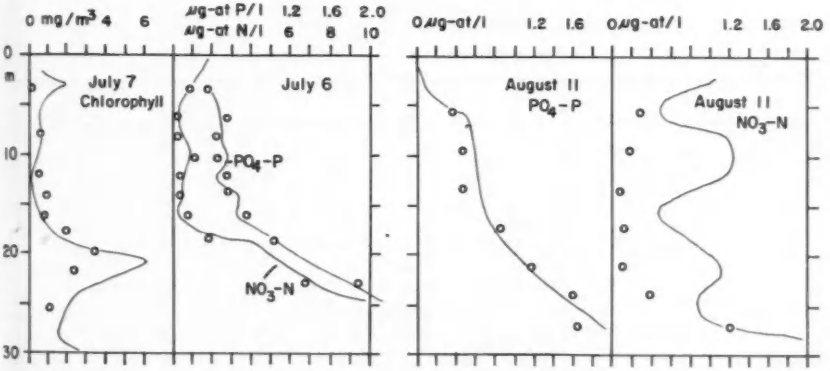

FIG. 1. Amounts of chlorophyll and nutrients in an unfertilized (control) polyethylene column (open symbols) and amounts in the middle basin of Ogac Lake (curves interpolated from seasonal series) on selected dates.

nutrient uptake or chlorophyll development in the early part of the experiment, but that nitrate concentrations were smaller in the column than in the lake later in the season. Development of zooplankton populations was similar in the lake and unfertilized column (McLaren, 1969).

RESULTS

CHLOROPHYLL

Seasonal changes in chlorophyll in the middle basin of the lake and fertilized column in 1962 are summarized in Fig. 2.

The production season clearly began in early June, when melting of snow and the appearance of holes and fissures in the ice allowed some light to penetrate. The ice began to break up and move in early July. A well-defined maximum of chlorophyll descended from near the surface in early June to below

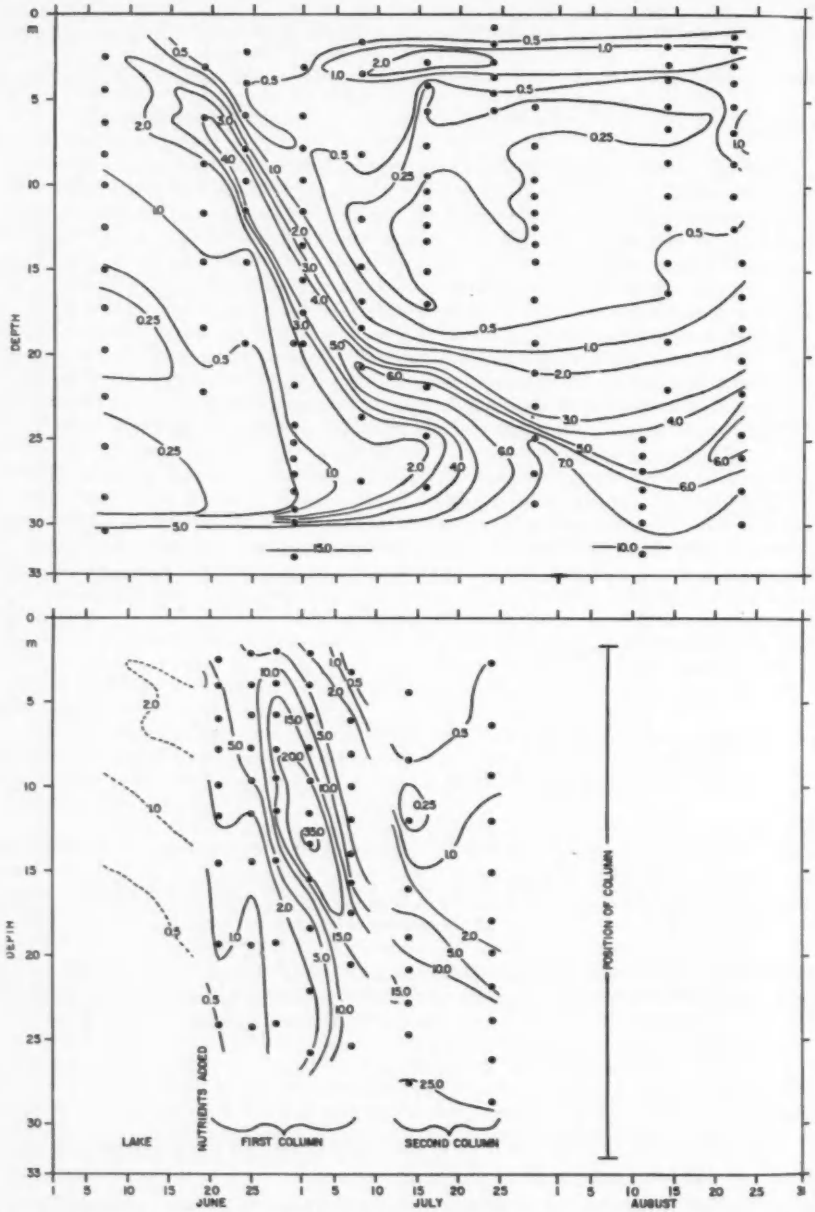

FIG. 2. Seasonal and vertical changes in chlorophyll concentration in the middle basin of Ogac Lake (*above*) and fertilized columns (*below*). Isopleths in mg/m³ based on samples at each point.

10 m in early July, and chlorophyll concentration remained high in deeper water through summer. Although chlorophyll was almost absent at mid-depths during summer, a flourishing phytoplankton population apparently developed and was sustained in the halocline at 2–3 m. A distinct increase occurred in mid-depths during August.

Changes in chlorophyll per m^2 are shown in Fig. 3. Values below 29 m were not integrated, as the chlorophyll near and in the anoxic water may have been "dead." Water from the boundary of anoxic water often left reddish-brown matter on filters, possibly from photosynthetic sulfur bacteria (Trüper

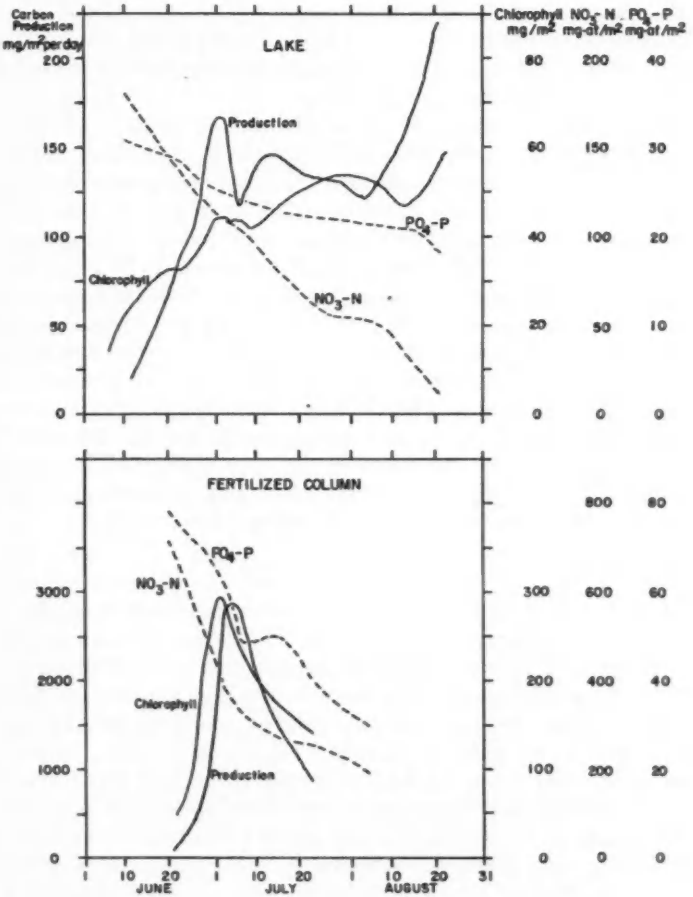

FIG. 3. Seasonal changes in chlorophyll, primary production, nitrate, and phosphate. Curves represent integrated values between 0 and 29 m from Fig. 2, 4, 5, and 6.

and Genovese, 1968). Much of the variation shown in Fig. 2 is masked in Fig. 3, which indicates relatively uniform concentrations per m^2 from late June through mid-August. The mean standing crop of chlorophyll between June 20 and August 20 was about 45 mg/m^2.

Fertilization caused an enormous increase in chlorophyll (Fig. 2), with an integrated maximum of about 300 mg/m^2 (Fig. 3). The peak was relatively short-lived, so that by late July the total amount of chlorophyll was only about three times as large in the column as in the lake. The average chlorophyll concentration during the fertilization experiment was about 170 mg/m^2. If it is assumed that chlorophyll concentration continued to decline at the same rate indicated in Fig. 3 until August 20, the average concentration was only about three times as great as in the lake during the same period.

Chlorophyll concentration at 2.6 m in the fertilized column was only about 0.5 mg/m^2; there was no evidence of the maximum found in the halocline of the lake at the same depth at this time.

Small numbers of chlorophyll measurements were made in all three basins of the lake in 1957 (McLaren, MS, 1961, table VII). These indicate a general decline at mid-depths in summer and sustained high values near the boundaries of anoxic depths (20 m in the outer basin, 30 m in the other two), but are not sufficiently closely spaced in depth or time for an accurate appraisal. Counts of phytoplankton cells in vertical net samples from 20 m to the surface (McLaren, 1969, fig. 4) showed peaks in all basins in late June and early July. Numbers were sustained through July and August in the outer basin, but not in the middle and inner basin, where virtual disappearance in midsummer was followed by peaks in late August; this latter pattern resembles that of chlorophyll in mid-depths in 1962 (Fig. 2). Chlorophyll at 2–3 m was only 0.4–0.9 μg/liter in early July, and was unmeasurable in the only sample for this depth in summer (August 3 in the inner basin; see McLaren, MS, 1961, table VII). This suggests that the flourishing of phytoplankton at the halocline, so conspicuous in 1962 (Fig. 2), did not occur in 1957.

Production

Production in the middle basin in 1962 is summarized in Fig. 4. In spite of large gaps in the series of measurements, the general pattern of production can be seen to have followed the more complete series of chlorophyll values in Fig. 2. In the middle basin, there was a descending maximum of production that tended to follow the upper regions of the descending chlorophyll maximum, perhaps a result of self-shading. Sustained high production in deeper waters seems safely inferred from the high values in early July and early August, and the high chlorophyll levels between these dates. Continued high production in the chlorophyll-rich halocline at 2–3 m seems confirmed by the single measurement for late July, made in association with the experiments in the fertilized column. A distinct recovery of production rates at mid-depths seems indicated for August 14–20, preceeding the increase in chlorophyll (cf. Fig. 2, 4).

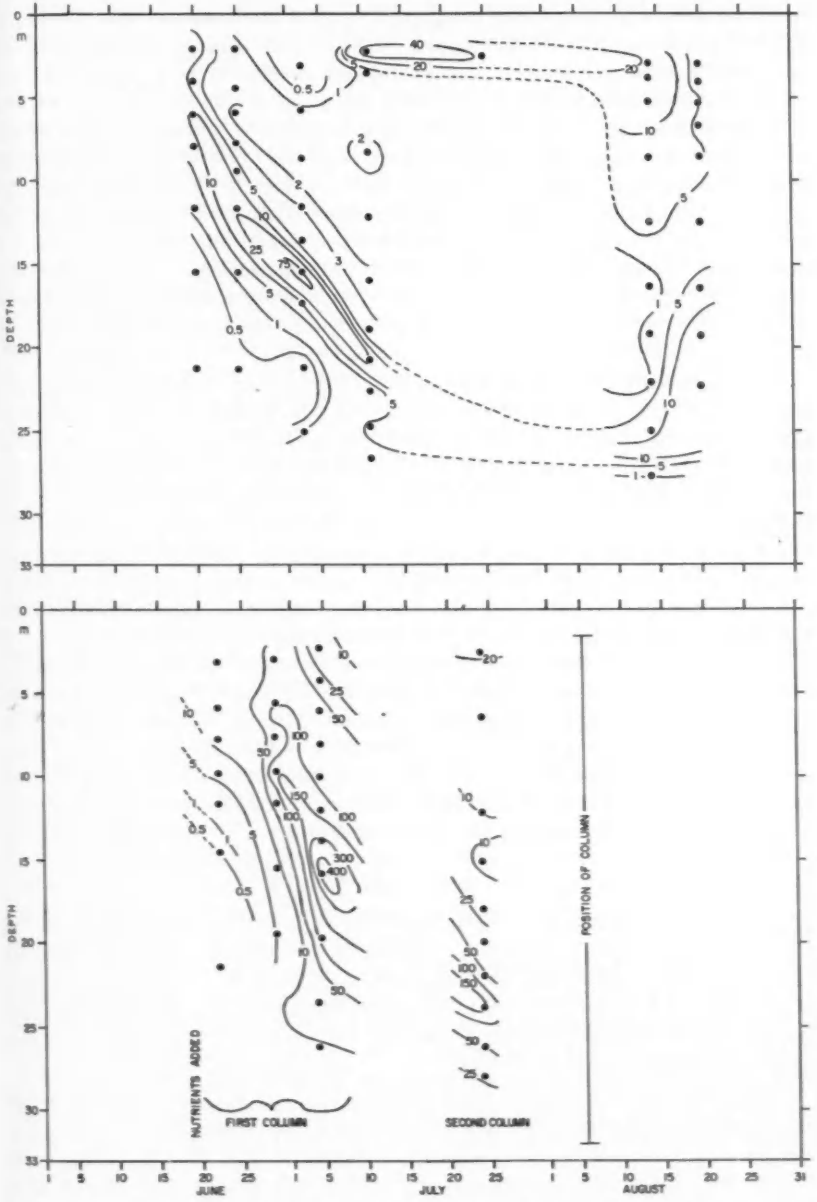

FIG. 4. Seasonal and vertical changes in primary production in the middle basin of Ogac Lake (*above*) and fertilized columns (*below*). Isopleths in mg C/m³ per day are based on 24-hr experiments at each point.

The values in Fig. 4 are integrated to give production per m^2 in Fig. 3. For the period of July 11 to August 14 estimates were made by joining up isopleths in the manner indicated by the broken curves for 5 mg/m^3 per day in Fig. 4. Production at mid-depths between the isopleths for 5 mg/m^3 per day was assumed to be 1 mg/m^3 per day. Although this assumption is unlikely to be very accurate, there are no indications in the chlorophyll measurements (Fig. 2) that large "bursts" of production between July 11 and August 14 are unaccounted for. Production for the season June 10 to August 20 is thus estimated as averaging about 120 mg/m^2 per day, for a total of about 9 g during the season. If it is assumed that the production fell off during late August to become negligible after mid-September (see indications of this in nutrient values below) then total production can be estimated as approximately 12 g/m^2 per year.

Production in the fertilized column (Fig. 4) also followed the pattern suggested by the chlorophyll estimates (Fig. 2), with maximum production again occurring slightly above the depth of maximum chlorophyll concentrations. The peak of production occurred *after* the peak in chlorophyll concentration; this may have been partly due to self-shading, but it should be noted that the ^{14}C experiments on July 5–6 were carried out when the wasting ice was beginning to move, allowing the full sunlight of those dates to penetrate deeply for the first time. Peak production values in early July were about 17 times as high in the column as in the lake, and mean production estimate during the experiment was about 10 times as high, for a total of about 45 g/m^2. If production continued to decline at the rate indicated on Fig. 3, a total production between June 20 and August 20 of some 60 g/m^2 is indicated, or about seven times that achieved in the lake during the same period. Presumably these are overestimates of the effect that fertilization would have on the lake as a whole, since the columns received oblique illumination through more transparent lake water, although this may have been restricted by growth of periphyton in the column later in the experiment.

Nitrate

Although nitrate cannot have been the only source of nitrogen for the phytoplankton, nitrite was almost absent in the middle basin on June 12, 1962, where it ranged from 0 to slightly more than 0.1 μg-at NO_2–N/liter at six depths between 2 and 29 m. Amounts of ammonia were not estimated, but almost all available nutrient N at the beginning of the productive season may have been oxidized to nitrate.

The amounts of nitrate on June 10–12, 1962, between 2 m and the boundaries of anaerobic water (about 20 m in the outer basin and 30 m in the other two basins) were about 155, 190, and 200 mg-at NO_3–N/m^2 in the outer, middle, and inner basins respectively. This means that nitrate was slightly more concentrated on a volume basis in the outer basin, and it was much more concentrated at shallower depths (McLaren, 1967b, fig. 20).

The ultilization of nitrate in the middle basin clearly paralleled the descending maximum of production in summer, and great restrictions of production and chlorophyll accompanied the virtual disappearance of nitrate from mid-depths in summer (Fig. 2, 4, 5). The distinct recovery of nitrate in early August coincided with a burst of production at this time (Fig. 3) and the rapid decrease of nitrate at all depths by August 20 may have foretold the end of the season of production in the lake. (The lower values on August 11 in the unfertilized "control" column (see Fig. 1) may reflect a slight lag in regeneration, but the explanation is not clear.) The sustained production in the halocline (Fig. 2, 4) seems clearly related to the levels of nitrate near the surface, which must have been constantly replenished. In spite of this apparent replenishment near the surface and the brief recovery at mid-depths in early August, nitrate disappeared from the water column at a relatively constant rate of about 2.3 mg-at NO_3–N/m² per day between mid-June and mid-August.

The concentrations of nitrate at the beginning of the fertilization experiment were rapidly used up, but never reached the very low values found at mid-depths in the middle basin, and showed some recovery by mid-August (Fig. 5). The slowing down of utilization is evident on Fig. 3, which indicates a rate of loss of some 25 mg-at NO_3–N/m² per day in late June and 4 mg-at/m² per day in mid-July.

Phosphate

Phosphate/nitrate ratios were higher in all basins of the lake than in most marine environments (McLaren, 1967b). The overall P:N ratio (assuming all N was NO_3) at the beginning of the season of about 1:5 (Fig. 3) was also higher than for most phytoplankton (Strickland, 1960).

Because samples were not sufficiently close-spaced, the presence of a phosphate minimum, as found near the anoxic depths in the middle basin, could not be confirmed in the other two basins (McLaren, 1967b, fig. 20). Thus initial amounts of phosphate in the three basins can only be compared in a relative fashion, by assuming for purposes of calculation that *no* minimum existed between 25 and 30 m in the middle basin. On this basis, amounts of phosphate per unit area were almost equal in the outer and middle basins, and about 15% less in the inner basin.

The decline of phosphate (Fig. 6) followed the descending maximum of chlorophyll (Fig. 2) and production (Fig. 4). Phosphate recovered at mid-depths before nitrate in early summer, and declined after nitrate in late summer, and thus phosphate was not as well correlated with the increase in production in late summer. The phosphate minimum between 25 and 30 m (Fig. 6; see also McLaren, 1967b, fig. 21) became less pronounced later in the season. Note the virtual disappearance of phosphate from near the surface in summer, whereas levels of nitrate were maintained. Despite variations in vertical distribution, the phosphate in the water column as a whole (Fig. 3) declined relatively constantly, at about 0.17 mg-at PO_4–P/m² per day leaving substantial quantities at the end of the season.

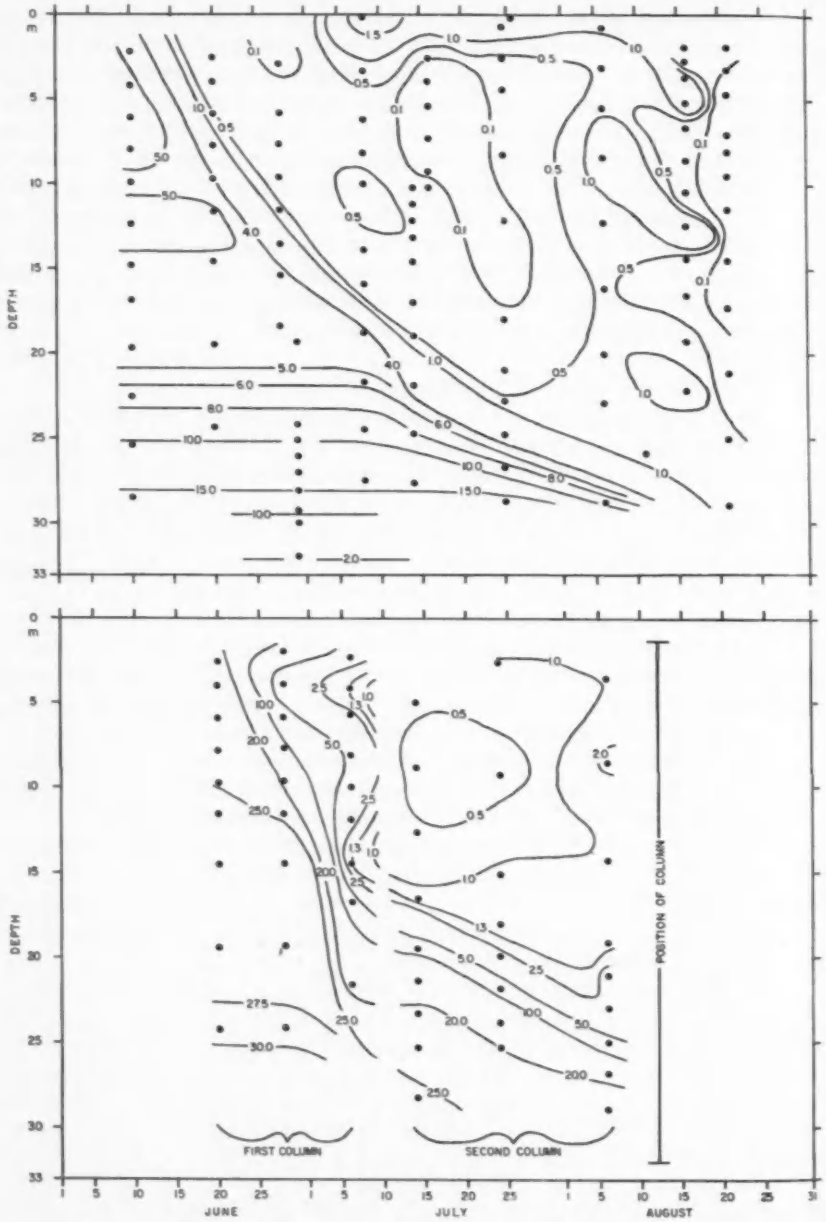

FIG. 5. Seasonal changes in nitrate concentrations in the middle basin of Ogac Lake (*above*) and fertilized columns (*below*). Isopleths in mg-at N/m³ based on samples at each point.

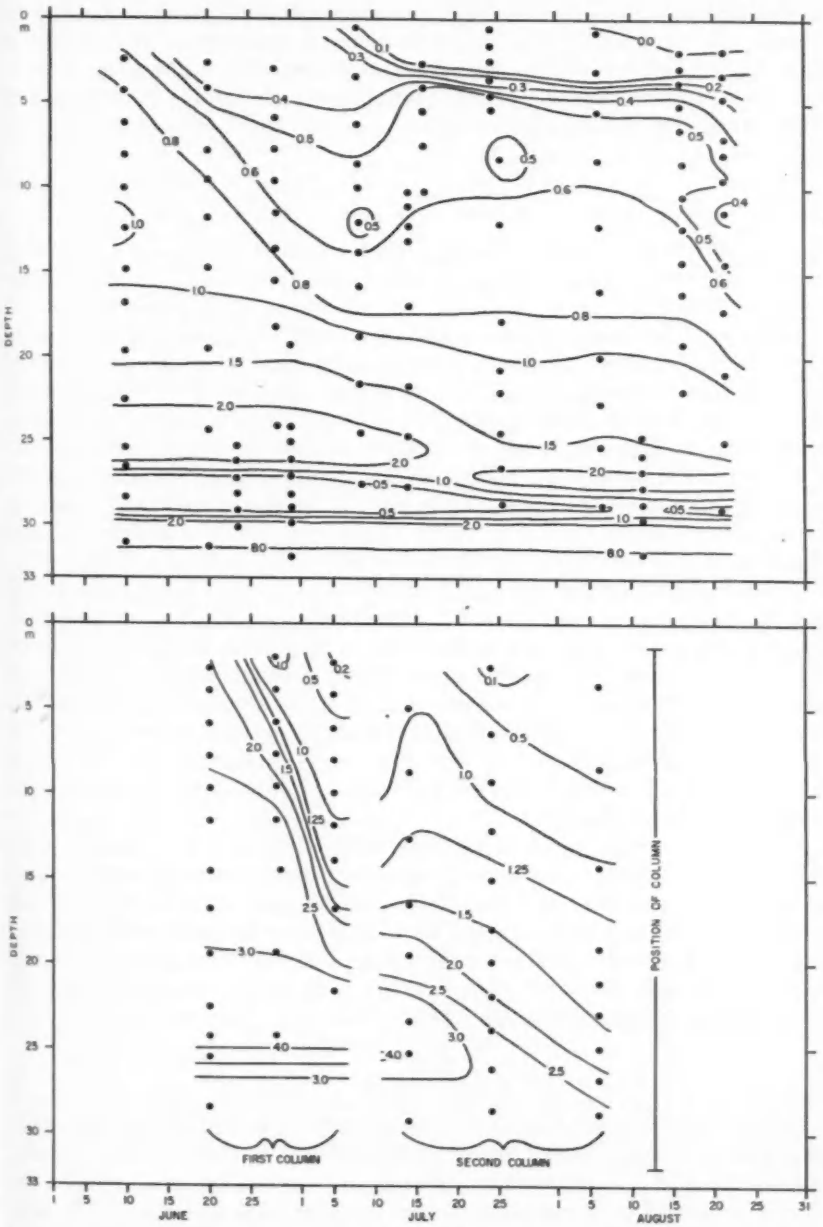

FIG. 6. Seasonal and vertical changes in phosphate concentration in the middle basin of Ogac Lake (*above*) and fertilized columns (*below*). Isopleths in mg-at P/m³ based on samples at each point.

Phosphate in the fertilized column again reflected the patterns of chlorophyll and production. The apparent marked recovery at mid-depths in July (Fig. 6) was probably not a result of (unknown) initial differences between the two fertilized columns, as phosphate continued to decline in deep waters. The overall rate of decline was about 0.96 mg-at PO_4–P/m^2 per day between late June and early August.

Oxygen

General characteristics of oxygen distribution in Ogac Lake have been summarized by McLaren (1967b). Seasonal changes in the lake and fertilized column in 1962 are shown in Fig. 7. Because of the strong stratification, all changes of oxygen concentration below a few meters must be biogenic. Figure 8 summarizes these changes as the integral in mg-at/m^2 of all changes, positive and negative, between 2.5 and 29 m. Oxygen production in mg-at should be almost equivalent to net production of carbon with correction for photosynthetic quotients, but there are several sources of oxygen consumption. An attempt has been made to estimate the *relative* effect of zooplankton by summing estimates to the $\frac{2}{3}$ power of carbon content of each individual plankter in the water column (McLaren, 1969), since metabolic demand for oxygen might be expected roughly to follow such a "surface law" (Zeuthen, 1953). The increments of oxygen and net carbon production were similar at the beginning of the season in the lake and the fertilized column, after which oxygen consumption greatly exceeded primary production (Fig. 8). This cannot be accounted for by the zooplankton alone which increased only slightly whereas oxygen increments decreased rapidly, but is presumably attributable to microbial and chemical demand. In the lake, the second peak of oxygen production occurred at the beginning of the rise in primary production (Fig. 8), which may again have reflected microbial and chemical demand for oxygen after a period of organic enrichment.

The oxygen cycle in the three basins of the lake in 1957 is described by McLaren (MS, 1961). Samples were too widely spaced in depth and time to allow a detailed analysis of seasonal change, but the gross pattern is summarized in Fig. 9. The peaks in early summer were followed by decreases in midsummer and recoveries in late summer, corresponding with rate changes in 1962 (Fig. 8). The cycle was somewhat earlier in the inner basin, where ice departed earlier and phytoplankton peaked earlier (McLaren, 1969, fig. 4).

DISCUSSION

Ogac Lake is unproductive compared with most inshore marine environments, even those in the arctic (Steeman-Nielsen, 1968). This is clearly a consequence of its isolation from the sea and meromictic nature. Different rates of regeneration of available nitrogen and phosphorous presumably lead to a greater loss of the organic nitrogen into the anaerobic depths. Thus available nitrogen is scarce and limiting. Presumably the nutrient quantities in

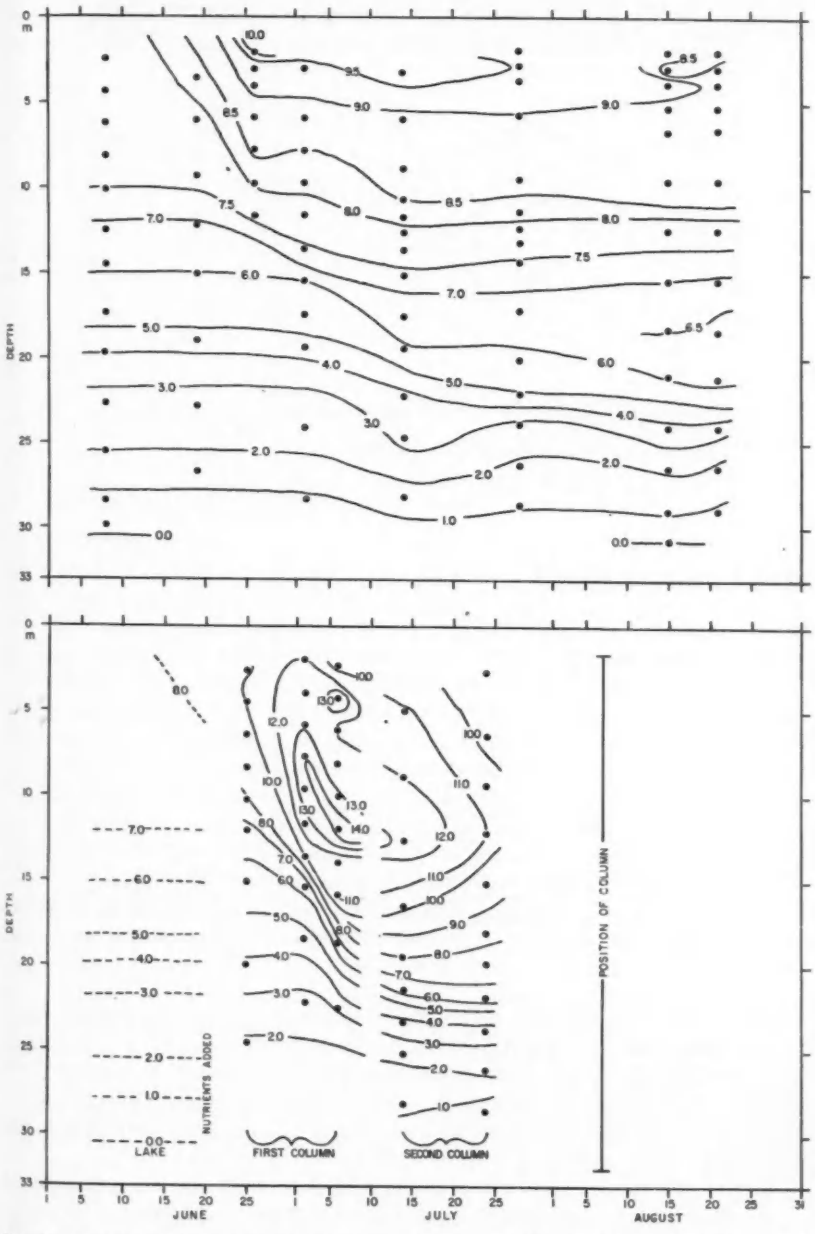

FIG. 7. Seasonal and vertical changes in oxygen concentration in the middle basin of Ogac Lake (*above*) and fertilized columns (*below*). Isopleths in liters/m³ based on samples at each point.

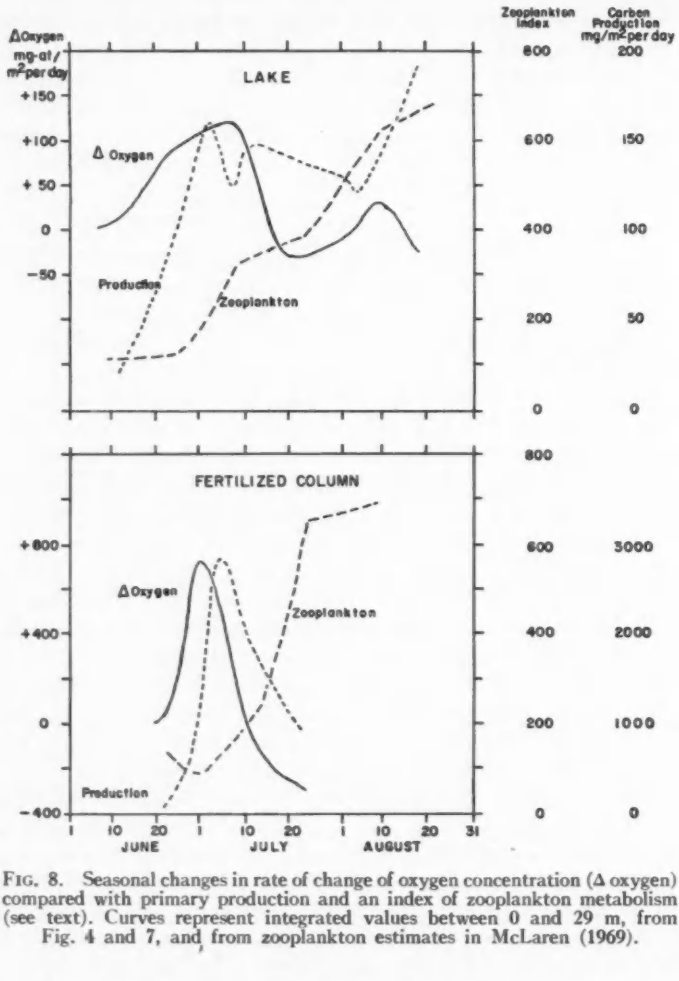

FIG. 8. Seasonal changes in rate of change of oxygen concentration (Δ oxygen) compared with primary production and an index of zooplankton metabolism (see text). Curves represent integrated values between 0 and 29 m, from Fig. 4 and 7, and from zooplankton estimates in McLaren (1969).

the lake are set over the long term by loss to the depths and by inflows from the sea, which may be largely depleted of nutrients in summer (McLaren, 1967b), but rich in zooplankton (McLaren, 1969). The roughly parallel rates of utilization of nitrate and phosphate in the fertilized column (Fig. 3), where the original P:N ratio was changed from about 1:5 to 1:10, also emphasizes the limiting role of available N in the lake.

Production in the lake was thus largely dependent on the available N at the end of winter, presumably almost all in the form of nitrate. The slight recovery of nitrate at mid-depths in early August led to an increase in production that must have been short-lived (although observations are not availa-

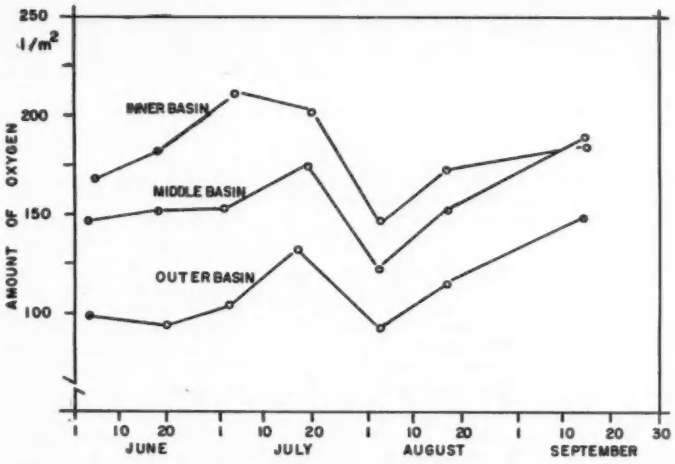

FIG. 9. Amounts of oxygen in water columns of the three basins of Ogac Lake in 1957. Integrated from values given by McLaren (MS, 1961, fig. 20).

ble from late August), because nitrate in the water column as a whole continued to decline and was almost absent by August 21.

The increase of production in the fertilized column by about an order of magnitude from a four-fold increase in nitrate suggests that a substantial fraction of the production was supported by regeneration of nutrients, which became quite evident in mid-depths in early August (Fig. 5). Since zooplankton metabolism was probably smaller in the fertilized column (Fig. 8), the regeneration must be attributed largely to chemical and microbiological sources. In spite of such regeneration, much of the added nutrient must have been lost by sinking in particulate form. This is characteristic of fertilization experiments, and doubtless extreme in the highly stratified waters of Ogac Lake.

Zooplankton grazing appears to have little influence on the patterns of production in the lake. Herbivorous zooplankton were concentrated at the halocline and in deeper water (McLaren, 1969), where chlorophyll concentrations and production were sustained by the availability of nutrients.

A special feature of the lake was the sustained production at the halocline near the surface during summer of 1962. Here, contrary to the pattern in deeper water, nitrate was sustained and phosphate almost disappeared after mid-July. Zooplankton concentrated at the halocline in summer (McLaren, 1969) may have supplied some nutrients, and the possibility of nitrification cannot be ignored. It is also noteworthy that the freshwater layer was deeper in 1962 than in 1957, and that much of the fauna in the narrow zone of *Fucus* at 2–3 m was killed by this freshening in 1962. Decay in this zone may have supplied much nutrient, entrained in the outflowing fresh waters of the surface, and mixed down into the halocline. This would explain the apparent dearth of chlorophyll at the halocline in 1957, when no such freshwater kill occurred,

and the low values of chlorophyll in 1962 near the tops of the unfertilized column (Fig. 1) and fertilized column (Fig. 2), which were cut off from possible replenishments. Production in the haloclines of such lakes might merit closer study.

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Free Fatty Acids of Herring Oils: Possible Derivation from both Phospholipids and Triglycerides in Fresh Herring[1]

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Addison, R. F., R. G. Ackman, and J. Hingley. 1969. Free fatty acids of herring oils: possible derivation from both phospholipids and triglycerides in fresh herring. J. Fish. Res. Bd. Canada 26: 1577–1583.

The free fatty acids (FFA) of nine commercially produced Nova Scotia herring oils were compared with the overall oil fatty acid compositions. Results were consistent with the FFA having arisen primarily through hydrolysis of phospholipids, but additionally from hydrolysis of triglycerides. Phosphorus levels indicate that hydrolysis of phospholipids probably occurs by enzyme action, before oil production rather than after, but suggest that in some instances FFA may be formed by slow chemical hydrolysis of phospholipids after oil production.

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INTRODUCTION

Production of oil from herring (*Clupea harengus*) is of growing importance in the Atlantic Provinces of Canada. Most plants operate only on a seasonal basis but in both summer and winter can produce oils with free fatty acid (FFA) levels not exceeding 1%, and in some periods consistently of 0.5% or lower (Ackman, 1967). Production facilities usually preclude refining of the oils beyond removal of solids and water and a final centrifuge polishing. Removal of FFA by alkali refining is generally left to the purchaser since this is preferably carried out immediately before further processing. The FFA level of the oil is, however, of interest to the primary producer, since within certain limits, it is one of the factors governing the price of the oil. Although at the time of production FFA levels may be low, there are occasional reports of unexpected increases in FFA during prolonged storage or even during shipment. As part of a study of the factors governing FFA levels in fish oils, we have examined in detail the composition of FFA from some herring oils produced in Nova Scotia during summer 1968.

EXPERIMENTAL

Samples of herring oils produced during summer 1968 were obtained from a commercial source. Date of catch, fish size, and location of catch are as follows:

June 26 Fish 10–12" (25–30 cm), caught off Yarmouth, N.S.
June 27 Fish 10–12" (25–30 cm), caught off Yarmouth, N.S.

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July 6 Fish 10–14" (25–35 cm), caught off Yarmouth, N.S.
July 15 Fish 10–18" (25–46 cm), caught off Jeffrey Bank, U.S. coast
July 23 Caught off Portland, Me.
Aug. 13 Fish 10–14" (25–35 cm,) caught off Yarmouth, N.S.
Aug. 22 Caught off Yarmouth, N.S.
Aug. 28 Fish 10–12" (25–30 cm), caught off Yarmouth, N.S.
Sept. 23 Fish 10–14" (25–35 cm), caught off Maine coast

Iodine values (IV:Wijs) and % FFA levels (by AOCS method No. Ca 5a-40) were determined on receipt of samples (normally 3 days after production). These were then stored at 0 C, under nitrogen, for up to 3 months, pending further analyses.

The composition of the oils was determined by gas–liquid chromatography (GLC) of their fatty acid methyl esters, as described elsewhere (Addison et al., 1968). The FFA fractions were isolated from 25-g samples of the oils by saponification and extraction (Ackman et al., 1962). Final traces of triglycerides were removed from the FFA by chromatography on Sephadex LH-20 (Addison and Ackman, 1969). The recovered FFA were esterified and analysed by GLC as for the oils.

Phosphorus (P) levels (%) in the oils were determined by the method of Allen (1940).

RESULTS AND DISCUSSION

The IV, % FFA, and % P contents of the oils are shown in Table 1. In general, IV calculated from fatty acid analyses agreed with or were slightly

TABLE 1. Iodine values, free fatty acids, and phosphorus content of herring oils.

Oil (date produced 1968)	IV		% FFA		% P	Max FFA % derived from phospholipid
	Wijs	Calc.	AOCS	Isolation		
June 26	125.1	126.8	1.22	1.30	0.059	Approx 1.11
27	120.3	118.6	0.54	0.39	0.014	" 0.26
July 6	125.0	117.4	0.94	0.90	0.010	" 0.19
15	123.5	117.0	0.57	0.52	0.030	" 0.56
23	141.0	142.8	0.99	0.88	0.013	" 0.24
Aug. 13	115.5	103.5	0.51	0.49	0.003	" 0.06
22	110.7	103.3	0.86	0.69	0.005	" 0.09
28	110.2	105.6	0.33	0.24	0.010	" 0.19
Sept. 23	131.4	121.5	1.20	1.36	0.007	" 0.13

lower than those determined by the Wijs method; possible reasons for the discrepancies have been discussed by Ackman and Eaton (1966). % FFA levels, calculated from the extraction and column chromatographic data, also agreed fairly well with those determined at an earlier time by the AOCS method. The significance of the % P levels, and their equivalent % FFA levels, is discussed further below.

Fatty acid analyses of the oils and of their FFA are shown in Table 2. The oils were similar in composition to those described by Ackman and Eaton (1966). For those oils prepared from fish caught over the season in the same

area (Yarmouth, N.S.) there was a slight drop in IV due to a reduction in polyunsaturate levels in the period June–August. This has been noted in previous years (Ackman, 1967).

The composition of the FFA differed considerably from that of the "parent" oil in respect to several major components which may be reliably quantitated. The main differences lay in two groups of fatty acids. The monoenes — 16:1,[2] 20:1, and 22:1 — were noticeably lower in the FFA than in the parent oils. The ubiquitous 18:1 was also generally about 20% lower in the FFA than in the oil, except in the exceptionally high IV oil of July 23. The latter may have been produced from sardine-size herring. The polyunsaturates, mainly 20:5 and 22:6, were markedly higher in the FFA. Palmitic acid (16:0) was also higher in the FFA than in the parent oil. Differences observed in the calculated IV of the FFA roughly paralleled those of the parent oils.

The composition of the FFA was *basically* similar to that peculiar to marine fish phospholipids (cf. Addison et al., 1968) and implied that the FFA had a phospholipid origin. The fatty acid compositions of phospholipids and triglycerides, laboratory-extracted from fresh whole herring (Drozdowski and Ackman, 1969), are therefore shown in Table 2 for comparison with the mean oil FFA composition. The fatty acid distributions for triglycerides are not uniquely comparable, since season, area of catch, and method of lipid extraction (or oil production) differed, but the oil FFA composition suggests a mixture of fatty acids from phospholipids and triglycerides. The hydrolysis of muscle phospholipid in lean fish is familiar, but fatty fish have been less thoroughly studied (Olley and Duncan, 1965; Bligh and Scott, 1966). Our results are in agreement with the recent observation by Bosund and Ganrot (1969) that frozen storage of Baltic herring is accompanied by both phospholipid and triglyceride hydrolysis, and a similar process may occur in frozen Newfoundland capelin (Ackman et al., 1969). The data in Table 2 suggest that the composition of FFA in herring oils produced from relatively fresh fish (perhaps 24 hr out of water) could be accounted for by assuming that 75% arose from phospholipid and 25% from triglyceride hydrolysis (calculated only for major acids in final column of Table 2). Bosund and Ganrot (1969), following changes in lipids from the same batch of fish throughout their experiments, concluded that phospholipid hydrolysis produced 75% of the FFA in light muscle and 45% of the FFA in dark muscle.

Phosphorus levels in the oils were analysed in an attempt to decide whether phospholipid hydrolysis occurred before or after oil production. If enzymatic phospholipid hydrolysis occurred before oil production, residual P (as glycerophosphate or related water soluble compounds) would probably be washed out of the oil. However, if any phospholipid remaining in the oil were hydrolysed chemically, residual P would probably remain in the oil, possibly dissolved in the small amount of water usually present or dispersed in a micelle. The results of the P analyses (Table 1) were not conclusive. Most values lay around

[2]Shorthand notation for chain length:number of double bonds.

TABLE 2. Fatty acid composition of lipids, oils, and

Peak[a]	June 26 oil		June 27 oil		July 6 oil		July 15 oil		July 23 oil	
	Oil	FFA	Oil	FFA	Oil	FFA	Oil	FFA	Oil	FFA
12:0	0.1	tr[d]	0.2	–	0.1	tr	0.1	tr	0.2	0.1
13:0	0.1	–	tr	–	tr	–	–	–	tr	–
14:0	8.5	5.9	8.1	4.6	8.0	5.8	8.1	4.8	9.8	4.8
Br 15:0[e, f]	0.5	0.1	0.3	–	0.5	0.5	0.6	tr	0.3	tr
15:0	0.6	0.6	0.4	0.5	0.5	0.5	0.7	0.4	0.3	0.4
Br 16:0[f]	tr	–	0.1	–	tr	tr	tr	tr	tr	tr
16:0	14.4	17.9	14.6	20.0	13.9	18.5	14.0	21.4	14.1	20.5
16:1ω7	13.6	5.7	14.9	5.7	12.0	7.4	12.4	6.7	10.3	4.9
16:2ω4	0.2	0.4	0.5	0.2	0.8	0.2	0.7	0.2	0.8	tr
16:3ω4	0.1	0.1	0.2	tr	0.4	0.2	0.6	tr	0.8	0.2
16:4ω1	0.8	0.3	1.2	tr	0.8	0.3	0.6	0.2	1.5	0.1
17:0	0.8	0.2	0.4	0.1	0.2	0.2	0.2	0.7	0.3	0.4
17:1ω8	0.3	0.1	0.4	0.1	tr	tr	tr	tr	0.2	tr
18:0	0.9	2.1	0.8	2.7	0.7	1.6	0.5	2.8	0.5	2.2
18:1ω9	13.1	9.6	16.1	12.1	13.3	11.8	12.8	11.5	9.4	10.6
18:2ω6	1.2	1.1	1.2	1.3	1.1	0.9	1.0	0.9	1.1	0.5
18:3ω6	–	tr	tr	–	tr	tr	tr	–	tr	tr
18:3ω3	0.6	1.1	0.6	0.7	0.7	0.5	0.8	0.6	0.9	0.5
18:4ω3	3.3	3.7	2.2	2.0	2.7	2.4	2.7	1.5	3.5	1.2
20:1ω9	11.3	4.9	10.9	5.1	13.4	6.9	13.2	5.6	11.5	3.7
20:2ω6	tr	–	tr	–	tr	–	–	–	tr	tr
20:3ω3	–	–	–	–	tr	–	–	–	–	–
20:4ω6	0.2	0.7	tr	0.6	0.1	0.7	tr	0.8	0.1	1.3
20:4ω3	tr	0.5	tr	tr	tr	tr	tr	tr	0.1	0.1
20:5ω3	8.6	14.8	8.6	15.0	7.2	13.8	7.4	13.7	12.1	17.8
21:5ω2	tr	–	tr	tr	–	–	–	tr	tr	–
22:1ω11	14.0	5.0	13.7	5.6	18.2	8.4	18.4	6.3	15.3	4.2
22:5ω6	–	tr	–	–	tr	–	–	–	tr	tr
22:5ω3	0.7	1.5	0.3	1.3	0.6	0.2	0.6	0.5	0.6	0.9
22:6ω3	6.0	23.5	4.2	22.3	4.7	19.2	4.6	21.4	6.2	25.6
24:1	tr	–	tr	–	tr	–	tr	–	tr	–
Σ Sats.	25.9	26.8	24.9	27.9	23.9	27.1	24.2	30.1	25.5	28.4
Σ Monoenes	52.3	25.3	56.0	28.6	56.9	34.5	56.8	30.1	46.7	23.4
Σ Polyunsats.	21.7	47.7	19.0	43.4	19.1	38.4	19.0	39.8	27.7	48.2
IV (Calc.)	126.8	209.8	118.6	201.5	117.4	185.6	117.0	188.9	142.8	217.8
IV (Wijs)	125.1	ND	120.3	ND	125.0	ND	123.5	ND	141.0	ND

[a]Shorthand notation for chain length:number of double bonds, and position of ultimate
[b]From results of Drozdowski and Ackman (1969): PL = phospholipid, TG = triglyceride.
[c]Calculated as described in text from data of Drozdowski and Ackman (1969).
[d]tr = trace.
[e]Br = branched chain.
[f]May include multiple branched chain acids.
[g]ND = not determined.

free fatty acid fractions of oils from Atlantic herring.

Aug. 13 oil		Aug. 22 oil		Aug. 28 oil		Sept. 23 oil		Mean	Fresh herring[b]		FFA[c] (calculated)
Oil	FFA	Oil	FFA	Oil	FFA	Oil	FFA	FFA	TG	PL	
0.1	tr	0.2	tr	0.2	0.1	0.3	tr	tr	tr	tr	–
–	–	tr	–	–	–	–	–	tr	tr	tr	–
9.9	4.8	7.6	4.2	9.5	3.5	8.8	5.7	4.9	5.6	1.8	2.7
0.6	0.2	0.5	tr	0.7	tr	0.6	0.5	0.1	0.7	0.2	–
0.6	0.5	0.5	0.5	0.5	0.3	0.6	0.6	0.5	0.4	0.3	–
0.1	tr	0.2	tr	0.1	tr	tr	tr	tr	tr	0.2	–
15.0	21.2	13.0	24.3	14.4	18.8	13.5	19.8	20.3	12.5	21.4	19.1
13.5	6.1	10.4	7.5	13.1	6.2	7.0	5.1	6.1	13.6	4.6	6.8
0.7	0.3	0.5	0.7	0.2	1.0	0.4	0.4	0.4	1.4	0.7	0.8
0.3	0.1	0.7	0.7	0.2	0.7	0.4	0.2	0.2	0.8	tr	–
0.7	0.4	0.7	0.4	0.7	0.3	0.4	0.1	0.2	1.3	tr	–
0.1	0.3	0.4	0.5	0.5	0.4	0.4	0.3	0.3	ND[a]	ND	–
0.3	tr	tr	tr	0.5	tr	0.3	tr	tr	ND	tr	–
0.5	3.4	0.7	3.0	0.7	3.3	1.0	1.7	2.5	1.1	3.2	2.7
15.2	12.8	15.1	14.8	15.2	13.0	10.3	9.1	11.7	15.5	13.0	13.6
0.9	1.1	1.1	1.8	1.0	1.2	1.6	1.2	1.1	1.1	0.9	0.9
tr	tr	tr	–	tr	tr	tr	–	tr	0.2	0.1	–
0.5	0.4	0.5	0.8	0.5	0.5	1.2	0.6	0.6	0.3	0.3	–
1.9	1.2	1.4	1.2	1.9	0.8	2.8	2.0	1.8	1.2	0.2	0.5
12.8	4.2	14.9	4.0	12.4	6.5	12.6	4.8	5.1	13.7	2.4	5.2
tr	–	0.1	tr	–	tr	tr	–	tr	0.2	0.1	–
tr	–	tr	–	–	–	–	–	tr	tr	tr	–
0.1	1.2	tr	1.2	tr	0.9	0.1	1.0	0.9	0.3	1.4	1.1
tr	0.1	tr	0.6	tr	0.1	tr	tr	0.2	0.1	0.1	–
6.2	14.8	4.7	13.0	6.5	12.0	7.0	12.5	14.2	6.8	12.2	10.7
–	tr	tr	tr	tr	–	0.2	–	tr	0.2	0.2	–
16.3	4.9	22.8	3.5	16.8	9.9	22.8	7.5	6.1	19.4	1.6	6.1
–	–	–	tr	–	–	0.2	–	tr	tr	0.2	–
0.4	1.2	0.4	0.5	0.4	1.0	0.4	0.9	0.9	0.2	0.8	–
3.3	20.7	3.4	16.7	3.8	19.4	6.7	25.7	21.6	3.1	32.7	25.3
tr	–	0.2	–	0.2	0.1	0.3	0.3	tr	tr	1.3	0.3
26.9	30.4	23.1	32.5	26.6	26.4	25.2	28.6	28.7	20.3	27.1	–
58.1	28.0	63.4	29.8	58.2	35.7	53.3	26.8	29.1	62.2	22.9	–
15.0	41.5	13.5	37.6	15.2	37.9	21.5	44.6	42.1	17.2	49.8	–
103.5	193.1	103.3	172.7	105.6	182.0	121.5	205.5	195.2	ND	ND	–
115.5	ND	110.7	ND	110.2	ND	131.4	ND	ND	ND	ND	–

double bond relative to the terminal methyl group.

0.01% (a figure obtained for certain oils examined in 1959; N. Dambergs, personal communication) but in two instances (June 26, July 15) were well above this value. If we assume that this P was originally present as phospholipid (of molecular weight P × 25 of which 75% is fatty acid) complete hydrolysis of this phospholipid would yield the FFA levels calculated in Table 1 (final column). On this basis, in the two oils with high % P levels, the % FFA levels could be accounted for by assuming post-reduction phospholipid hydrolysis; in two other oils (June 27, August 28) assuming that only 75% of FFA arose from phospholipid, hydrolysis of phospholipids could at least partially explain the FFA levels. Nothwithstanding these results the details of fatty acid composition strongly suggest that triglycerides contribute to the FFA even in these four oils. It may be that this contribution takes the form of preexisting FFA in a metabolic lipid pool.

We have discounted the possibility that partial phospholipid hydrolysis (either before or after oil production) contributes significantly to FFA formation. The acids 16:0 and 22:6 are localized in the α and β positions respectively in most fish phospholipids (Brockerhoff et al., 1963; Menzel and Olcott, 1964) and the high level of both acids in the FFA suggests that both positions in the phospholipid molecule are hydrolysed. Furthermore, lysophospholipids apparently do not accumulate during frozen storage of fish (e.g., Bligh and Scott, 1966).

We therefore conclude that the FFA of these particular herring oils are produced mainly through hydrolysis of flesh phospholipids, and to a lesser extent, triglycerides, and that generally this hydrolysis probably occurs before or during oil production. It is, however, possible that in some instances phospholipids could be partially responsible for FFA formation in these oils after production.

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Differences Between Two Populations of Landlocked Atlantic Salmon (*Salmo salar*) in Newfoundland[1]

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LEGGETT, WILLIAM C., AND G. POWER. 1969. Differences between two populations of landlocked Atlantic salmon (*Salmo salar*) in Newfoundland. J. Fish. Res. Bd. Canada 26: 1585–1596.

Differences in growth rates, longevity, fecundity, and time of spawning between two populations of landlocked Atlantic salmon (*Salmo salar*) in Newfoundland were attributed to food quality and quantity. Salmon in Flatwater Pond, an oligotrophic lake with a poor invertebrate population and no forage fish, grew slowly (145 mm at age 2+, 245 mm at age 5+), suffered high mortality (approximately 60% in males after age 2+ and in females after age 3+), had very low fecundity (an average of 153 eggs per female), and were sexually mature by late August. Salmon in Gambo Pond, an oligotrophic lake with a good invertebrate population and an ample forage fish population in the form of *Gasterosteus aculeatus*, grew more rapidly reaching 157 mm at age 2+, 367 mm by age 5+, and 437 mm by age 8+. Longevity of the Gambo Pond stock was greater than that of Flatwater Pond (39.6% of the Gambo sample were older than 4+ years compared with 3.2% for Flatwater Pond). Gambo Pond salmon are not sexually mature until October.

Salmon in both lakes exhibited seasonal movement into deeper water when the surface warmed above 14 C. At Flatwater Pond this movement contributed to an early end to the growing season.

Scale reading was found to be an unreliable method for determining past spawning activity. Spawning marks were found on only 1 of 17 females known to have spawned previously.

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INTRODUCTION

DISPERSED THROUGH the more remote areas of Quebec, Labrador, and Newfoundland island are numerous populations of nonanadromous Atlantic salmon (*Salmo salar*). These fish have been considered to be subspecifically different from populations living in the northeastern United States (Jordan and Evermann, 1896–1900). They were designated by the subspecific name *ouananiche*, which is a corruption of the Montagnais Indian name for the fish (Chambers, 1896). In the northeastern United States, the nonanadromous Atlantic salmon is known as Sebago salmon. The Sebago variety has had a considerable amount

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of attention devoted to it and has been subjected to various management procedures. It is doubtful if any unmanipulated stocks still exist. By contrast, little has been published about the ouananiche, which differs superficially from the Sebago salmon in its smaller ultimate size.

This report concerns an investigation in 1963 and 1964 of the food, growth, reproduction, and survival of two populations of ouananiche from Newfoundland. The influence of environment on these parameters is described and differences in the two populations are discussed in terms of probable causal factors.

Flatwater Pond (49°47′N, 56°18′W), studied in 1963, is oligotrophic and has a surface area of 725.2 ha, a mean depth of 12.8 m, and a maximum depth of 33.6 m. Aquatic vegetation is sparse. The lake contains large numbers of *Salvelinus fontinalis* and *Salmo salar*. *Salvelinus alpinus* and *Anguilla rostrata* are also present.

Gambo Pond (48°40′N, 54°25′W), studied in 1964, is in reality two lakes linked by a narrow, shallow stream known as the "narrows." The two lakes are identified as north and south Gambo ponds. The north pond has a surface area of 1113.7 ha, a mean depth of 5.5 m, and a maximum depth of 12.2 m; south pond 958.3 ha, 14.9 m, and 42.7 m. Both ponds are oligotrophic and aquatic vegetation is sparse. Some *Vallisneria* sp. occurs in shallow areas and there is extensive growth of *Nymphaea* sp. in the "narrows" area. The fish fauna is partly temporary as there is access to the sea via Gambo Brook, which is 1 mile long, 50–150 yards wide, and has little gradient. *Osmerus mordax* is abundant in late fall, winter, and spring but returns to the sea early in the summer. *Salmo salar* and *S. fontinalis* are well represented by both freshwater and anadromous forms. *Gasterosteus aculeatus* is abundant in both lakes and *Pungitius pungitius* is well established in the "narrows." *Salvelinus alpinus* and *A. rostrata* are also present.

METHODS

The majority of specimens were collected in fine nylon gillnets ranging in stretch mesh size from 1.5 to 4.5 inches. A number of specimens in the 0+, 1+, and 2+ age-classes were collected by seining along the beaches and in tributaries. Rotenone was used to collect 0+ fish in Pine Brook, south Gambo Pond.

Each specimen was weighed to the nearest half gram. Fork lengths were recorded to the nearest millimeter. Scale samples were taken from a position midway between the anterior end of the dorsal fin and the lateral line. Scale mounts were prepared in the field using the method described by Power (1964). Age determinations were made using the scale method validated for freshwater Atlantic salmon by Havey (1959), except that the length-frequency method was employed for age-groups 0+ and 1+ from Gambo Pond. Stomach contents were analyzed using the frequency of occurrence method, which Hynes (1950) thinks gives an adequate picture of the diet when large numbers of fish are examined. Sex and degree of maturity were recorded. Fecundity was determined for Flatwater Pond fish by direct count of the mature eggs in 30 ripe females (16.0–20.7 cm) taken between August 20 and 28, 1963. In addition the egg production of two large females (35.6 and 66.0 cm fork length) was calculated from counts made of samples of the ovaries. It was assumed, since the females used in making these counts were mature, that the counts represent fairly accurately the number of eggs which these fish would shed at spawning,

and that errors due to the inclusion of atretic eggs (Vladykov, 1956) in the counts would be small. No estimates of fecundity were obtained for ouananiche of Gambo Pond because no females were sufficiently mature by August 28.

RESULTS AND DISCUSSION

Age and Growth

Ouananiche parr, like those of anadromous Atlantic salmon, generally live in running water where the adults spawn. No 0+ and few 1+ fish were found in either Flatwater Pond or Gambo Pond but 3+ fish were more numerous. A rotenone sample taken in Pine Brook, Gambo Pond, produced many 0+ and 1+ fish, taken to be ouananiche, and no fish older than 3+. It appears from this evidence that the majority of young ouananiche move into the lakes at age 2 or 2+, a few earlier, and some a year later.

Growth rates to age 2+ in the two areas investigated were similar, but at later ages Gambo Pond ouananiche grew faster than the majority of the Flatwater ouananiche (Table 1, Fig. 1). The exceptions were three large fish taken in Flatwater Pond and excluded from Fig. 1. These were a 6-year-old male weighing 2.35 kg, a 7-year-old female weighing 5.10 kg, and a 9-year-old female weighing 3.85 kg. The growth history of these specimens, determined by back calculation from scale measurements, was similar to the growth pattern of the Gambo population. Significantly each of these fish was feeding on young ouananiche when captured and this may be the reason they grew more rapidly than other members of the population, which fed on insects.

The age structure of the Flatwater Pond ouananiche population was markedly different from that of the Gambo Pond population (Table 1). Few Flatwater Pond fish survived beyond 4+. In the Flatwater Pond sample only 3.2% were older than 4+ years of age whereas 39.6% of the Gambo Pond sample were older than this.

Diet

Table 2 suggests that insects form the bulk of the diet of ouananiche at Flatwater Pond, their frequency of occurrence being over 90% in June and July and over 80% in August. During June and July, adult dipterans and coleopterans and adult and larval trichopterans predominated. Adult Bibionidae were the important group during these months, at which time adult diptera accounted for over 90% of the bulk of food consumed and many stomachs contained over 100 of these small flies. During August, there was a change from surface to bottom feeding with a consequent decline in the consumption of terrestrial insects. This was accompanied by an extreme reduction in the quantity of food in the stomachs. Fewer than 5% of the 100 stomachs examined in August were distended to the norm for June and July.

At Gambo Pond forage fishes formed the bulk of the diet with adult dipterans and trichopterans next in importance (Table 2). A point not evident in the table is that small ouananiche (10–20 cm) fed mainly on insects (a diet similar to that reported for all ouananiche in Flatwater Pond) but larger fish

TABLE 1. Age and growth of ouananiche from the two ponds.

	Age											
	0+	1+	2+	3+	4+	5+	6+	7+	8+	9+	10+	Total
Flatwater Pond												
No. of specimens	0	42	102	361	125	15	4	1	0	1	0	651
Mean fork length (*cm*)	–	8.7±0.3[a]	14.5±1.9	18.7±2.2	20.9±2.6	24.5±6.1	38.8±16.5	–	–	–	–	
Mean wt (*g*)	–	7.1	38.3	72.3	94.1	228.3	1937.7	5102.0	–	3855.4	–	
Gambo Pond												
No. of specimens	113	73	49	26	26	71	65	38	10	3	1	475
Mean fork length (*cm*)	5.0±1.2	8.0±1.5	15.7±1.4	20.5±2.8	32.2±3.8	36.7±2.3	34.9±5.9	42.1±8.6	43.7±12.1	53.2±9.4	–	
Mean wt (*g*)	1.7	6.6	49.9	107.1	470.2	571.9	714.8	863.4	1067.3	1958.7	1725.0	

[a]Standard deviation of the mean.

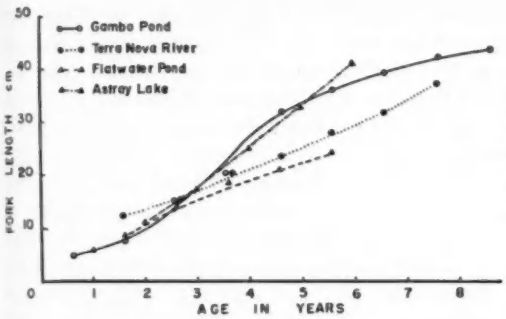

FIG. 1. Age and growth of ouananiche from four eastern Canadian populations. Terra Nova River data from Scott and Crossman (1964); Astray Lake data from Power (1958); Flatwater and Gambo Pond data from Table 1. Curves fitted by eye.

TABLE 2. Percentage frequencies of occurrence of various food items in the stomachs of ouananiche in the two ponds, showing changes in composition of diet over the summer. Numbers in parentheses after names of months are numbers of fish examined.

	Flatwater Pond			Gambo Pond		
Food item	June (100)	July (79)	Aug. (100)	June (83)	July (140)	Aug. (60)
Hirudinea	0.25		1.29		0.71	0.82
Oligochaeta						0.82
Mollusca	1.73	0.62	7.44			6.56
Crustacea	1.49	2.16	10.33			1.64
Arachnida	1.24	0.31				0.82
Insecta						
Orthoptera (A)*		0.31				0.82
Odonata (N)	0.50	0.93	1.24	2.41	0.71	
(A)	0.25	0.31				
Ephemeroptera (N)	4.70	11.11	3.31	8.43	0.71	
(A)	2.97	3.08	3.31			
Plecoptera (N)	0.72	1.23				2.46
(A)	1.24	0.33	0.41		1.43	
Trichoptera (L)	10.40	12.34	18.18	3.61	2.86	4.10
(P)	4.70	4.93	7.44			
(A)	10.40	10.49	7.85		9.99	10.66
Thysanoptera (A)						0.82
Lepidoptera (A)						1.64
Hemiptera (A)	4.21	1.85	3.72		0.71	9.84
Coleoptera (L)	0.25	0.31	12.40			1.64
(A)	14.11	10.80	2.47		3.57	4.92
Hymenoptera (A)	8.91	4.94	3.30		5.71	6.56
Diptera (L)	0.99	4.32	4.54			
(P)	3.47	4.01	5.76			
(A)	27.47	25.62	6.60	16.87	8.57	16.39
Fish						
Ouananiche			0.41			
Osmerus mordax				15.66	7.89	2.46
Gasterosteus aculeatus				49.39	56.43	22.95
Salmo salar						0.82
Pungitius pungitius					0.71	
?				3.63		3.26
Empty				15.66	8.73	17.80

*(A) = adult; (N) = nymph; (L) = larva; (P) = pupa.

showed a marked preference for forage fish. No changes in diet were evident during the summer. The apparent decline in the amount of fish eaten in August resulted from a higher percentage of small ouananiche in the August samples. Feeding rates were similar from June through August. Inclusion of forage fish in the diet, which were available all summer, accounted for this. Some variation in kinds of food organisms might be expected in late summer because of movement to cooler bottom waters, but this was not evident in the results.

Gasterosteus aculeatus was the major food item of the larger fishes in Gambo Pond during the summer. It was not uncommon to find 10 sticklebacks in one stomach and as many as 27 were recorded. Fish appeared to be actively selecting this food item. *Osmerus mordax* was eaten in the spring up until the time it returned to sea. Smelts occurred in 30% of the stomachs of 44 ouananiche examined between June 10 and 16, in 14% of 38 stomachs examined between June 17 and 23, and in 10% of 40 stomachs examined in the first week of July.

Sex Ratios and Reproductive Potential

At Gambo Pond sex ratios approximated unity throughout life (Table 3). At Flatwater Pond the percentage of males fell to between 15 and 20% after age 2+ indicating up to a 60% mortality among 2+ males. In older age-groups, the proportion of males in the population remained at about one-fifth, implying a similar high mortality among females beginning at age 3+. A study of the age of maturation of ouananiche from the two populations showed that the onset of sexual maturity coincided with the increased mortality described above. Most males were sexually mature at age 2+, and the majority of females matured at age 3+. Similar findings were reported for freshwater salmon by Blair (1937) and Warner (1962).

The most striking feature in the data on egg production for the 30 smaller ripe fish (16.0–20.7 cm) from Flatwater Pond is that the mean number of eggs produced was only 153 per female. Converted to mean number of eggs per pound the value is 883 (standard deviation 169). This value is very similar to the range (650–900 eggs per pound) reported for anadromous Atlantic salmon (Elson, 1957; Jones, 1959; Pope et al., 1961). One larger female of 35.0 cm fork length contained 890 eggs or 816 per pound; a second, 66.0 cm, contained 4726 eggs or 544 per pound.

Spawning Marks

Although spawning marks usually form on scales of Atlantic salmon that have spawned, they were found on the scales of only a small percentage of ouananiche that had presumably spawned.

In Flatwater Pond only one male out of 89 3+ years and older, and one female out of 115 4+ years and older showed spawning marks on their scales. Seventeen of the females bore unshed eggs in their body cavity, conclusive evidence that they had spawned the previous fall. Of the two fish displaying spawning marks on their scales, the larger, a female (5.10 kg, 70 cm fork

TABLE 3. Percentages of males of various ages in the two ponds (numbers in parentheses are numbers in samples).

Age (*years*):	0+	1+	2+	3+	4+	5+	6+	7+	8+
Flatwater Pond	50[a]	50[a]	39(102)	16(361)	20(125)	14(15)			
Gambo Pond	50[a]	50[a]	52(49)	47(26)	47(26)	52(71)	53(65)	47(38)	50(10)

[a]Theoretical value.

length) was 7+ years old and showed evidence of having spawned in its 6th and 7th falls. The smaller, a male (2.35 kg, 58.5 cm fork length) was 6+ years old and had spawned in its 5th and 6th years. It is probable that these fish had spawned earlier, but like the majority bore no record of the acts on their scales.

A similar situation was found at Gambo Pond. Of 90 females and 121 males 1 year or more beyond the minimum age for spawning, only 6 females and 21 males had spawning marks on their scales. None showed evidence of having spawned before age 5 yet many males and some females were mature at age 2+. Six fish showed more than one spawning mark and these indicated spawning had occurred annually for 2 or more years. Scales of these repeat spawners showed severe marginal resorption.

Movements in Relation to Water Temperature

During sampling, it became evident that ouananiche move into cooler and deeper water during the summer. In doing so they avoid high surface temperatures.

At Flatwater Pond, during June and early July, ouananiche were most numerous along the shore at depths up to 5 m. On July 11, the surface waters to a depth of 4 m warmed above 14 C. By July 26, few ouananiche could be taken in inshore waters of this depth. Nets set in deeper water were more effective.

In north Gambo Pond during June and early July, ouananiche were most abundant along the shore and over shoals at depths up to 6 m. On July 7, the lake warmed above 14 C at all depths and ouananiche gradually became available only in the deeper parts of south Gambo Pond. A definite decline in captures in the pond was evident by July 17 and during August it was difficult to take any ouananiche in the north pond. Additional evidence of movement came from increased angling catches in the "narrows" between July 10 and 20. Ouananiche from north Gambo Pond apparently moved out of this lake into the deeper cooler waters of south Gambo Pond. Similarly ouananiche became unavailable in the warm surface waters of south Gambo Pond but no difficulty was experienced in netting them during August in waters which were below 16 C.

GENERAL DISCUSSION

The two populations of ouananiche described in this paper differed in a number of respects. Growth rates and longevity were obviously different. Fecundity and time of spawning also differed. Most of these differences can be related directly or indirectly to food quality and quantity. The growth rate of the Flatwater Pond ouananiche (Fig. 1) is less than that reported by Scott and Crossman (1964) for ouananiche of the Terra Nova River, Newfoundland. Gambo Pond ouananiche grew more rapidly than those in Flatwater Pond but no faster than those of Astry Lake (Power, 1958), which is located much farther north at 54°35′N, 663°0′W.

As early as 1911, Dahl recognized the importance of food availability as a factor influencing the growth of fishes. Ouananiche of Flatwater Pond appear to experience difficulty in obtaining sufficient food. This is particularly true after the end of July. Regulation of water level in the lake has killed all trees within 20 to 30 yards of the water. In 1959, the forest around Flatwater Pond was destroyed by fire. As a result, there is little shelter or food in the area for terrestrial invertebrates, which form the bulk of the diet of ouananiche. This may also explain the paucity of aquatic insect larvae, pupae, and nymphs in the lake.

Ouananiche in Gambo Pond show no indication of suffering from reduced food availability during the growing season. Bottom samples taken from 11 stations in the two parts of the pond on September 21, 1965, by Mr J. Pippy, then of the Department of Fisheries of Canada, St. John's, Newfoundland, give evidence of a fairly large invertebrate population. The abundance of a few groups in the stomach contents of Gambo Pond ouananiche suggests that they are selective in their diet. This indicates a large biomass of invertebrates is available in Gambo Pond. More importantly, forage fishes are abundant in the Gambo Pond system. A difference in growth rate between ouananiche populations was found by other workers (Hoover, 1936; Havey, 1960; J. L. Brooks, personal communication) to be associated with the presence of fish in the diet.

The different growth rates of the ouananiche of Flatwater and Gambo ponds was presumably related to the quality of the food available to them. The growth rate for Gambo Pond ouananiche increased as the percentage of fish in the diet increased (Fig. 2). The retarded growth of the Flatwater

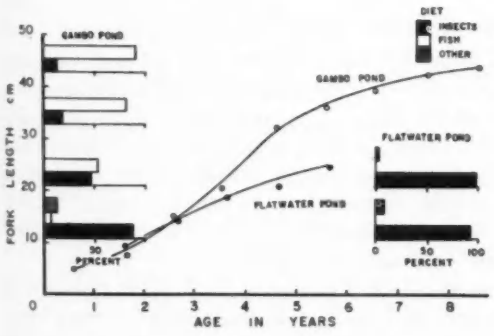

FIG. 2. Growth rates (curves) and diets (bars) of ouananiche at various lengths in two Newfoundland lakes.

fish was associated with the absence of fish from the diet. Further, the age of migration to the lakes (2+ years) coincided with the age at which fish were first utilized as food by Gambo ouananiche and at this age the Gambo fish first became larger than the Flatwater fish.

Summer movements of ouananiche were closely linked to changes in water temperature. Warner (1959) reported a similar movement for Sebago salmon

in Mud Lake, Maine. Where such movements result in a separation of the fish from its principal source of food, an early end to summer growth occurs. This apparently happened in Flatwater Pond, where movement into deeper water separated the ouananiche from terrestrial insects, their major source of food, and forced them to rely upon bottom fauna. Ekman dredge samples taken August 13, 1963 at numerous stations throughout the lake revealed a very low density of bottom organisms. The lack of food in ouananiche stomachs at this time indicates the fish weree xperiencing difficulty obtaining food in the deeper parts of the lake. In Gambo Pond movements due to water temperature did not separate the fish from their food. Forage fishes were available in the deeper parts of the lake and in addition the bottom fauna was much richer.

It was impossible to put numerical values on the degree of competition facing ouananiche in the two lakes. Similar fishing effort yielded about 4 times as many trout, ouananiche, and char in Flatwater Pond as in Gambo Pond, but the weight of fish caught in Gambo Pond slightly exceeded that taken in Flatwater Pond. The fish in Flatwater Pond were small and numerous and fed directly on invertebrates, whereas in Gambo Pond the majority of ouananiche were larger and made demands on the invertebrate fauna largely through the intermediary forage fishes. The ultimate demand on the invertebrates in Gambo Pond was presumably greater because of the longer food chain, but the abundance of forage fish enabled ouananiche to easily obtain adequate food. In addition at Flatwater Pond the ratio of ouananiche to other species was 1 to 2 whereas at Gambo Pond this ratio was 4.8 to 1. This apparent imbalance in the intensity of competition presumably accounts in part for the different growth patterns in the two populations.

Reduction in fecundity and in the size of spawning females in *Salmo salar* because of adoption of the freshwater habitat must be approaching the limit at Flatwater Pond. The average female produces only 153 eggs and few spawn more than once. Such reduction in individual egg production must be balanced by increased survival to maturity if the population is to be maintained. It is difficult to conceive a system in which eggs from small fish would experience a higher survival rate than eggs from larger fish unless survival is determined entirely by the carrying capacity of the environment. If this is so the higher reproductive potential of larger females may be largely wasted and serve only to protect against environmental extremes.

The early seasonal maturation of the Flatwater Pond stock is atypical and must represent an adaptation to the conditions peculiar to that lake. The separation of these fish from their food supply at the end of July, occasioned by their movement to deeper, cooler waters, forces an early end to the growing season. Sexual development must be well advanced by late July if maturity is to be attained. The early seasonal maturity of the Flatwater stock is correlated with an increase in post-spawning mortality. The spawning mortality of 2+ males in Flatwater Pond is approximately five times that experienced by males of equal age at Gambo Pond. Flatwater Pond females experience similar high mortalities upon reaching maturity at age 3+.

The lack of a consistent spawning mark on the scales of ouananiche is unusual. Blair (1937) suggested that in landlocked Atlantic salmon 1 year's spawning mark may be removed by resorption during the next spawning season but this is clearly not what is happening with the ouananiche. Jones (1949) found no evidence of spawning marks on the scales of precociously mature male parr of anadromous Atlantic salmon. It appears that freshwater salmon can react in the same way as male parr of anadromous stocks and spawn without experiencing scale resorption and the attendant formation of a spawning scar. Scale reading is not, therefore, a reliable method of recognizing previous spawning.

This investigation has provided new information on the relationship between naturally occurring, unmanaged ouananiche and their environment. It has shown the importance of a good food supply that is available to the fish throughout the growing season. Suitable forage fish are essential to good growth in ouananiche. Greeley (1948) and Hoover (1936) suggested *Osmerus mordax* as an ideal food. This investigation has shown that *Gasterosteus aculeatus* can also be utilized. Flatwater Pond is clearly a marginal habitat for the species, and the ouananiche have adapted to it in a number of ways including: slow growth and consequent small size; early seasonal maturation to coincide with the end of the period of adequate food supply; low fecundity presumably with a high rate of survival to maturity and a subsequent high mortality rate. Gambo Pond by contrast is a better environment and the ouananiche show none of the extremea daptations noted above, but are probably more typical of the numerous ouananiche populations existing throughout eastern Canada.

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Nucleotide Degradation in Frozen Swordfish Muscle

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Dyer, W. J., and Doris I. Hiltz. 1969. Nucleotide degradation in frozen swordfish muscle. J. Fish. Res. Bd. Canada 26: 1597–1603.

In frozen swordfish steaks, inosine monophosphate (IMP) dephosphorylation was active at −8 C and less so at −18 C. A loss of IMP at −26 C became apparent during a 2-year storage period. Rates of loss were about 0.24 and 0.029 μmoles per g per week at −8 and −18 C, the Arrhenius plot being linear over the temperature range 0 to −26 C. Inosine ribohydrolase was less active; nevertheless, about 2.5 μmoles per g of hypoxanthine accumulated in 2 years at −8 C. Taste panel tests indicated a storage life of 3 months at −8 C, 9 months at −18 C, and several years at −26 C. The loss of IMP was slightly slower than the associated taste panel score decrease and thus may have potential as an indicator of frozen storage quality in some fish species, though it did not prove useful for swordfish. Hypoxanthine formation at low storage temperatures is sufficiently slow to allow use of hypoxanthine as an index of prefreezing quality; however, red muscle must not be included in the sample because of its high initial hypoxanthine content, about 1.9 μmoles per g.

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INTRODUCTION

Use of hypoxanthine (Hx) and of other products of the postmortem nucleotide degradation sequence, from adenosine triphosphate through inosine monophosphate (IMP), inosine (Ino) to Hx, as spoilage indices has focused attention on the stability of these nucleotide compounds during frozen storage. In addition, any loss of IMP during frozen storage could result in flavor loss in the product. In cod, Jones (1965) reports that IMP phosphohydrolase is inactive at −30 C but that all the enzymes of the nucleotide degradation sequence are active down to −14 C, and that the sequence is similar to postmortem degradation in unfrozen tissue (except that the formation of guanine was noted). Connell (1967) and Connell and Howgate (1968) find that after as long as 50 weeks, Hx does not change in frozen cod of various degrees of initial freshness at either −14, −22, or −29 C, and they suggest that the discrepancy with Jones' finding at −14 C is accounted for by the fact the latter used prerigor frozen fish.

In swordfish (*Xiphias gladius*) IMP is degraded slowly, in 4–5 months, at −4 C (Dyer et al., 1966); Ino accumulation with very slow Hx formation shows that the Ino ribohydrolase activity is lower than that of the IMP phosphohydrolase. The rates were little affected by initial quality as determined by varying periods of storage in ice prior to freezing, suggesting that endogenous rather than bacterial enzymes were involved. In the present work, enzymic

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nucleotide degradation rates were examined in frozen swordfish steaks stored at −26, −18, and −8 C, and compared with taste panel quality assessments.

EXPERIMENTAL

Thirty-six steaks, 2 cm thick, were cut from an 88.5 kg swordfish, landed iced by a commercial vessel at Halifax (June 22, 1966). The extreme tail- and head-ends of the carcass were discarded. Each steak was halved along the dorsal septum; the pieces were packaged individually in sealed polyethylene bags and quick-frozen (1.5 hr) in a plate freezer (Dole Freeze-Cel) followed by storage at −8, −18, and −26 C. Previous results had shown little variation in nucleotide components with steak position in the carcass (Dyer et al., 1966), but to avoid any positional bias equal numbers of steaks from the anterior, mid-, and posterior regions were stored at each temperature.

At each sampling period, composite samples of approximately 10 g each were cut from the ordinary and from the red muscle of each of three half-steaks representing the anterior, mid-, and posterior sections; the remaining portions of these half steaks were used for taste panel testing. Initial samples were prepared similarly, one prior to freezing and another, from the opposite halves of the same steaks, just after freezing (about 2 hr out of the freezer). Taste panel evaluation, perchloric acid extraction, and analysis of the neutralized extracts for total purine compounds, IMP, and Hx were carried out as previously described (Dyer et al., 1966). The taste panel could detect no change in the samples stored at −26 C for up to at least a year, and thus these served as taste panel controls for the samples stored at −8 and −18 C (fresh top-quality swordfish was not available for such controls over the period of the experiment).

RESULTS AND DISCUSSION

Changes on Freezing

Freezing did not change the IMP, Ino, and Hx concentrations in either ordinary or red muscle (Fig. 1). The initial nucleotide pattern in the fish used was similar to swordfish iced for about 7–10 days by comparison with fig. 1 of Dyer et al. (1966).

Changes During Frozen Storage

IMP phosphohydrolase is quite active in ordinary muscle at −8 C (Fig. 1), and less so at −18 C, with a degradation of 0.029 μmoles IMP per g per week vs. an initial rate of about 0.24 at −8 C. Contrary to previous reports (see Introduction), some activity becomes evident at −26 C after a year or more of storage. About one-third the initial IMP is dephosphorylated after 2 years; "goodness of fit" of the regression line (Snedecor, 1956) showing significance ($P = .05$) in the period from 31 to 97 weeks, with a slope of 0.021 μmoles per g per week. In previous work also, no change was found up to 17–22 weeks storage of swordfish at −26 C (Dyer et al., 1966).

Ino tends to accumulate on long storage at the three temperatures used, with an initial rapid increase at −8 C, its formation from IMP being more rapid in this species than its degradation to Hx.

The increase in Hx is not significant at −26 C, but a slow increase occurs at −18 C. At −8 C the initial rate is five times as fast as at −18 C, resulting in an accumulation of about 2.5 μmoles per g over 2 years storage, the rate decreasing after the 1st year. Thus the Ino ribohydrolase is much less active.

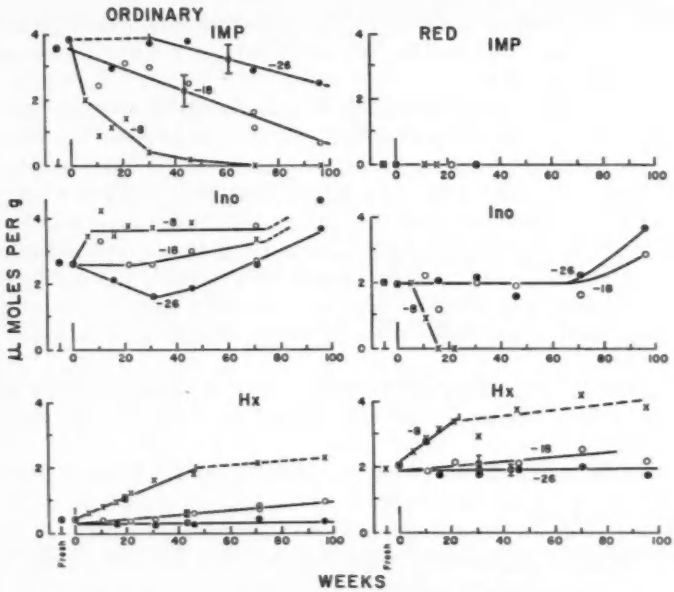

FIG. 1. Nucleotide changes in ordinary and red muscle of frozen swordfish steaks stored at −8 (×), −18 (○), and −26 C (●). Regression lines (linear) have been drawn for IMP and Hx, and the 95% confidence interval of the mean at the midpoint is shown. The regression equations are:

Ordinary muscle:

IMP −18 C	$Y = 3.58 - 0.029X$	($P = 0.005$, $n = 8$)
IMP −26	$Y = 4.54 - 0.021X$	($P = 0.05$, $n = 4$), over range 31–97 weeks
Hx −8	$Y = 0.46 + 0.0316X$	($P = 0.001$, $n = 7$), over range 0–46 weeks
Hx −18	$Y = 0.32 + 0.0064X$	($P = 0.001$, $n = 8$)
Hx −26	$Y = 0.30 + 0.0007X$	(P = n.s.)

Red muscle:

Hx −8 C	$Y = 2.13 + 0.060X$	($P = 0.001$, $n = 5$), over range 0–22 weeks
Hx −18	$Y = 1.87 + 0.0071X$	(P = n.s.)
Hx −26	$Y = 1.89 + 0.0009X$	(P = n.s.)

approximately one-eighth, than the IMP phosphohydrolase in frozen swordfish muscle at −8 C.

Recently, similar IMP dephosphorylation has been noted in frozen chicken muscle (Davidek and Khan, 1968), with slight degradation occurring at −20 C, about 40% in 50 weeks, and less than 10% loss at −80 C after 60 weeks. Ino accumulation occurred at low temperatures in chicken as in the swordfish muscle, but at −5 C, the maximum was reached at about 10 weeks followed by a rapid decline. At −4 C in swordfish, however, Ino continued to accumulate up to at least 4–5 months (Dyer et al., 1966), again emphasizing the variation in activity of the various nucleotide degradative enzymes in muscle of different species (Fraser et al., 1968b) and animal groups. Another instance of variation appears in the work of Sameshima (1965) and of Ohta et al. (1967), who found

little IMP loss in bonito and skipjack muscle after slow freezing and storage at −10 or −20 C for 2 months, but in the following 2 months storage at −10 C a rapid decline occurred.

In the red muscle of swordfish, IMP had already been decomposed at the initial sampling as previously observed (Dyer et al., 1966). Net turnover of Ino and Hx production during frozen storage occur at rates similar to the ordinary muscle, though initial Hx production at −8 C is slightly faster in the red (Fig. 1). Note, however, that the initial level of Hx in red muscle is about 1.9 μmoles per g, approximately 1.5 μmoles per g above the level in ordinary muscle, in agreement with previous results on swordfish and mackerel (Dyer et al., 1966; Fraser et al., 1968a). It follows, therefore, that for optimum results red muscle should be carefully excluded during sampling when Hx is used as a quality test.

The effect of temperature on the rate of IMP dephosphorylation in swordfish was examined further by plotting log rate vs. reciprocal of temperature ($\frac{1000}{K}$). Data at 0 and −4 C from previous results (Dyer et al., 1966) were also included (Fig. 2). A good straight-line fit resulted, yielding an Arrhenius activation energy of 25 Kcal per mole over the range 0 to −26 C. Similar plots

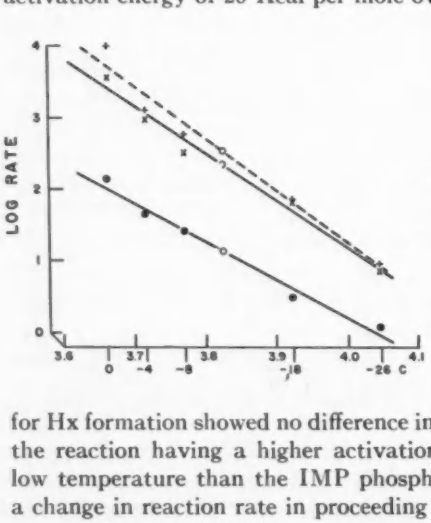

FIG. 2. Arrhenius plot of log rate of dephosphorylation of IMP and of Hx accumulation vs. inverse of temperature ($\frac{1000}{K}$) over the temperature range 0 to −26 C, where K is temperature in Kelvin units. ●——● IMP E_A = 24.6 (±1.9); ×——× Hx — ordinary muscle E_A = 30.3 (±2.1); +– – –+ Hx — red muscle E_A = 33.5 (±3.4), where E_A is Arrhenius Activation Energy in Kcal per mole with its SD in parentheses.

for Hx formation showed no difference in rate between ordinary and red muscle, the reaction having a higher activation energy and being more inhibited at low temperature than the IMP phosphohydrolase. There was no evidence of a change in reaction rate in proceeding from the unfrozen to the frozen state, as was observed in chicken muscle (Davidek and Khan, 1968), nor of the activation at temperatures just below freezing sometimes observed in deteriorative reactions in frozen muscle (see Dyer et al., 1966). This could indicate that IMP phosphohydrolase and the other nucleotide-degrading enzymes are not bound within cellular particles such as lysosomes, the membranes of which could suffer damage by the freezing and storage process resulting in liberation of the enzymes to the substrate sites (see Dyer, 1967).

Storage Temperature and Changes in Texture and Taste (Organoleptic)

The regression lines for taste panel scores of texture and of taste with time using individual scores indicate a linear relation (Fig. 3*a*, *b*). The goodness of fit was better than $P = 0.001$ (except for −26 C where $P = 0.005$) showing

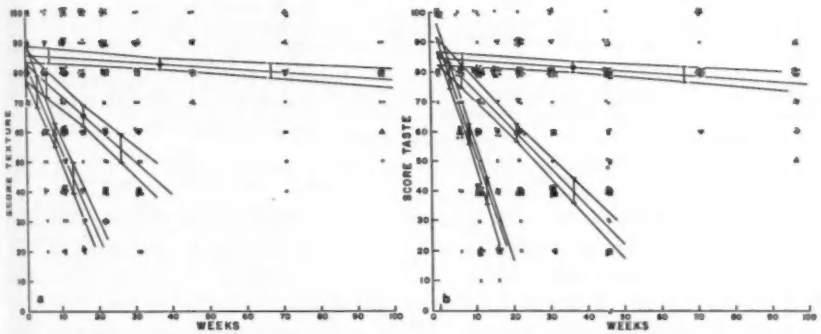

Fig. 3. Texture score (*a*) and taste score (*b*) in frozen swordfish steaks stored at −8, −18, and −26 C for up to 97 weeks. Individual scores for the eight panel members are shown (approx 24 for each sampling time at each temperature). Regression lines with 95% confidence intervals of the mean are plotted. Texture: −8 C (×) Y = 82.9–2.90X (n = 92); −18 (○) Y = 83.0–1.10X (n = 97); −26 (●) Y = 86.0–0.087X (n = 187). Taste: −8 (×) Y = 90.5–3.84X; −18 (○) Y = 86.7–1.29X; −26 (●) Y = 84.5–0.081X.

good consistency in the taste panel scores, and the 95% confidence intervals of the means (from ±2.3 to ±5.3 at the mean point) are also low. Taste shows a tendency to decrease slightly more rapidly than texture, but trends are similar.

The rejection level (taste panel score of 40) for the texture and taste respectively is reached in 15 and 13 weeks at −8 C, and in 39 and 36 weeks at −18 C. At −26 C, extrapolation yields a keeping time of 10–10½ years! The rather poor storage life of only 9 months at −18 C (0 F) is remarkable and indicates that holding frozen swordfish at this temperature is poor practice indeed. Possibly, this short storage life at −18 C might be improved if oxygen-impermeable packaging were used.

IMP and Hx as Potential Indices of Frozen Storage Quality Change

The IMP loss (ordinary muscle) appears to occur only slightly more slowly than the taste deterioration, and thus should be considered as a possible indicator of quality loss due to frozen storage. However, the regression lines of the relation between taste scores and IMP show that IMP loss is comparatively less at −18 than at −8 C (Fig. 4) indicating that a lowering of temperature slows IMP dephosphorylation more than quality loss as measured by taste scores.

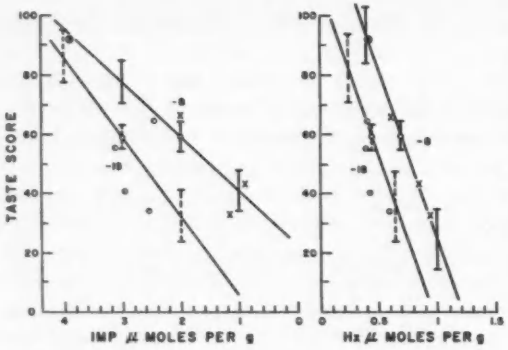

FIG. 4. Regression lines of taste scores (Y) vs. IMP (X) and Hx (X_1) in frozen swordfish steaks stored at −8 and −18 C; 95% confidence intervals of the mean are shown. For clarity, average taste scores only for each sampling period are plotted, but individual scores were used for calculation of the regression lines.
IMP −18 C (○) $Y = (-21.1) + 26.8X$;
IMP −8 C (×) $Y = 22.4 + 18.5X$;
Hx −18 C (○) $Y = 111 - 115X_1$;
Hx −8 C (×) $Y = 139 - 114X_1$.

Thus either IMP level or amount of IMP dephosphorylation will not yield a good estimate of quality loss due to frozen storage in swordfish except perhaps when storage temperature is accurately known. It seems probable that the natural strong flavor of the swordfish obscures any flavor loss resulting from the decrease in IMP. Because of this, and since the enzymic rates in the various stages of the nucleotide degradation sequence vary greatly between species, it is possible that in certain species with a bland flavor, the IMP dephosphorylation during frozen storage at various temperatures may correlate better with changes in the taste scores than it does in the swordfish.

Insufficient Hx is formed during frozen storage for its use as an index of cold storage deterioration (Fig. 1), in agreement with Connell's (1967) results on frozen cod. Consequently, due to the inactivity of the inosine ribohydrolase at low temperatures, Hx can be used as an indicator of pre-freezing quality on frozen fish stored at temperatures below −8 C, with little danger of Hx production during frozen storage of samples awaiting analyses. Inclusion of red muscle, however, must be avoided as pointed out above because of its much higher initial Hx content, and the resulting relatively large effect of inclusion of variable amounts of red muscle in the sample. In species with more active Ino ribohydrolase enzymes, e.g. redfish (Fraser et al., 1968b), formation of Hx may occur more rapidly at high storage temperatures (above about −10 C) and during the freezing process, especially at slow freezing rates.

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Reduction of Zooplankton Standing Stocks by Predaceous *Cyclops bicuspidatus thomasi* in Marion Lake, British Columbia[1]

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The standing stock of the copepod *Cyclops bicuspidatus thomasi* Forbes in Marion Lake, B.C., was observed during the summers of 1966 and 1967. Stage IV copepodids excysted during April and moulted to adults, which produced eggs in May. The new generation developed to the copepodid IV stage by midsummer, when about 85% of the animals moved to the bottom and encysted. The copepodids of stage IV and V and the adults are predators. When each group of the prey of *C. b. thomasi* was offered separately in the laboratory, these predators fed best on their own nauplii and copepodids, diaptomid nauplii, and rotifers, but ate few diaptomid copepodids and cladocerans. When offered a mixture of prey at the lake, the predators ate nauplii in the same quantities as in the laboratory but, contrary to the laboratory results, very few rotifers. During the summer of 1967 *C. b. thomasi* copepodids IV and V and adults were estimated to have eaten 31.0% of the *C. b. thomasi* nauplius standing stock, and 30.2% of the diaptomid nauplius standing stock.

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INTRODUCTION

PREDATORY COPEPODS have often been recognized as important components of aquatic food chains, but most of our present knowledge about their diets is qualitative rather than quantitative. Fryer (1957a, b) has reported that the food of carnivorous cyclopoids includes (*a*) nauplii and copepodids of their own species; (*b*) nauplii and copepodids of other copepod species; and (*c*) cladocerans, dipterous larvae, ostracods, rotifers, and "indeterminate mush" (which may be attributed to protozoa and other soft-bodied organisms). Algal cells also occur, but whether they are ingested directly, or are the gut contents of some filter-feeding prey is conjectural.

During this study several groups of potential planktonic prey were offered to copepodids IV and V and adults of *Cyclops bicuspidatus thomasi* Forbes in the laboratory and at Marion Lake, and their rates of predation were quantitatively determined. An estimate of prey mortality in the lake, due to *C. b. thomasi* predation, was then calculated by combining these feeding data with data on the standing stocks of predators and prey in Marion Lake.

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MATERIALS AND METHODS

Samples for population estimates were taken throughout the spring, summer, and fall of 1966 and 1967 at a station near the deepest area of the lake (station 9′, Efford, 1967). The depth at the station was 5 m. Most of the samples were collected at about 2300 hr during 1966, and at about 1000 hr during 1967. An electric pump, capable of pumping 33.3 liters per minute, was used at 1-m intervals from 0.5 to 4.5 m, and each sample was collected by filtering 100 liters of water through a plankton net with mesh apertures of 73 μ. The number of animals in each sample was estimated by counting all of the animals in $\frac{1}{20}$th of a sample. The total numbers of rotifers, cladocerans, diaptomid nauplii, and diaptomid copepodids were recorded and the *C. b. thomasi* population was enumerated under the headings of nauplii I, II, III, IV, and V, copepodids I, II, III, IV, and V, adult females, adult males, and eggs.

For the laboratory determination of feeding rates a total of five *C. b. thomasi* predators (copepodids IV and V and adults) were placed in a 65-ml bottle, and a known concentration of prey added. The bottle was filled with lake water which had been filtered through a membrane filter with a pore diameter of 0.8 μ, and the bottle was sealed and placed in a constant temperature water bath at 17.5 $\pm$ 1.0 C in semidarkness. After 24 $\pm$ 2 hr all the animals were removed by filtering through a plankton net with an aperture of 54 μ, and rinsed into a petri dish. The survivors were then counted under a binocular microscope. When rotifers were used as the prey, the animals remaining were allowed to settle in a 100-ml settling chamber before being counted.

At Marion Lake, mixed groups of prey were offered to *C. b. thomasi* IV and V and adults during the summer of 1968. Known numbers of both predators and prey were removed from the lake and immediately placed in large plastic petri dishes containing 50 ml of lake water which had been filtered through a membrane filter with a pore diameter of 0.80 μ. The dishes were kept at lake temperatures, in the dark, for 24 hr. Both predators and prey were then killed and counted in their petri dishes under a binocular microscope.

Experiments to ascertain whether algae were a possible food source for the copepodids IV and V and adults of *C. b. thomasi* were similar in technique to those of Richman (1966) except that (*a*) an automatic particle counter was used to count algal cells; and (*b*) the bottles were rotated at 0.2 rpm rather than at 1.8 rpm. The algal cells were obtained from Dr J. Stein, Department of Botany, The University of British Columbia, and were grown on a soil medium under artificial light at room temperature.

RESULTS

C. B. THOMASI STANDING CROP

Due to high winter flushing rates, Marion Lake is only habitable to planktonic organisms from March or April until September or October (Efford, 1967). During 1966 and 1967 the flow rate was high in the winter (Fig. 1) and a large proportion of the plankton produced during this period was washed out of the lake almost immediately. During April the flow rate decreased, and the lake began to stabilize; at this time the lake temperature also increased.

In 1967, no animals were taken on or before April 3; however, on April 27, the concentration of stage IV copepodids was 1800 per cubic meter and no animals of any other stage were found, indicating that diapause terminated about mid-April when the flow decreased and the temperature increased.

Most of the stage IV copepodids moulted to adults by mid-May and these produced eggs by the end of May (Fig. 2). In early June the eggs hatched to nauplii. The nauplii moulted to copepodids by the end of June and by the middle of July most of the population had reached the copepodid IV stage. Between July 17 and July 24, 1967, more than half of the stage IV copepodids

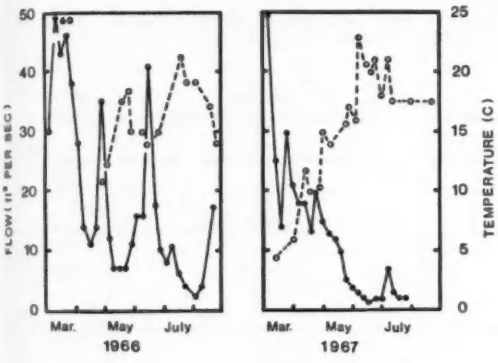

FIG. 1. Amounts of water entering Marion Lake (*solid lines*), and temperatures at 2 m depth (*broken lines*), during the study periods in 1966 and 1967. Flow was monitored automatically.

encysted. The remaining stage IV copepodids and a few stage V copepodids encysted near the end of August. During 1966, encystment of stage IV occurred regularly throughout both July and August.

Development time from egg to copepodid IV was approximated by using the length of time between the peak of egg production and the peak of the copepodid IV standing crop. This interval was about 45 days, which is longer than the 28–35 days for *Cyclops bicuspidatus* development from egg to adult reported by Ewers (1936); however, his animals were reared at room temperature whereas the Marion Lake animals experienced temperatures ranging from 5 to 23 C, and according to Coker (1934) and Ewers (1936) low temperatures increase the development time. During 1967 *C. b. thomasi* required, on the average, 16 days to moult through five nauplius stages, and 22 days to moult through the copepodid I, II, and III stages. Throughout the remainder of this paper these periods are called the nauplii and copepodid "residence" times.

The predaceous forms of *C. b. thomasi*, copepodids IV and V and adults, appeared in the plankton of Marion Lake in April and May of 1966 and 1967. The total predator population was highest during July of both years and decreased during August as the copepodids of stage IV encysted (Table 1).

FEEDING RATES IN THE LABORATORY

After the findings of Klugh (1927), I first assumed that *C. b. thomasi* was a herbivore or omnivore. To test this theory, seven types of algae found extensively in Marion Lake were fed to the *C. b. thomasi* copepodids IV and V and adults. The algae used were: *Chlorella pyrenoidosa* (UBC 395), *Ochromonas* sp. (UBC 242), *Merismopedia* sp., *Chalmydomonas* sp. (UBC 66), *Cryptomonas* sp. (UBC 12), *Scenedesmus quadricauda* (UBC 614), and *Chromulina scherffellii* (UBC 244). In no instance were the counts from the bottles containing animals different from the counts in the controls and consequently it may be concluded that *C. b. thomasi* copepodids IV and V and adults do not feed upon any of the seven cell types offered. Since these algae are representative

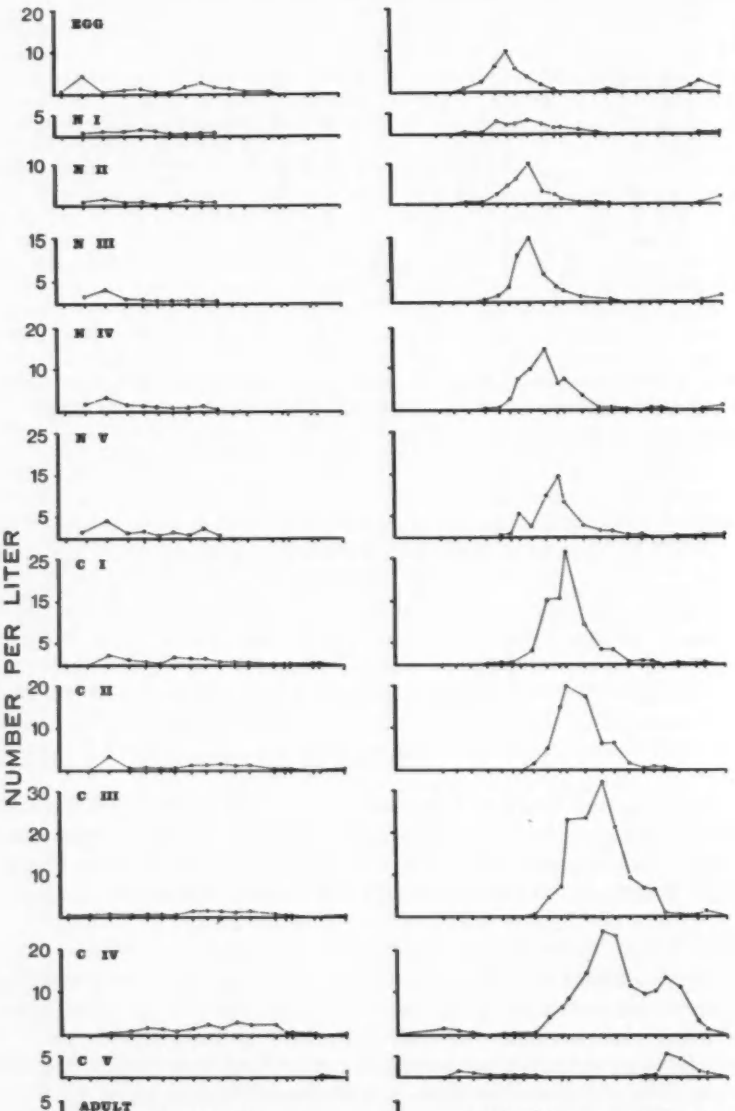

FIG. 2. Standing stocks of *C. b. thomasi* in various stages during 1966 and 1967.

TABLE 1. Standing stocks (numbers per liter) of *C. b. thomasi* predators (copepodids IV and V and adults) in Marion Lake during 1966 and 1967.

Date	No. per liter	Date	No. per liter
1966		1967	
May 16	0.12	Apr. 3	0.00
19	0.67	25	1.29
26	1.12	May 2	2.62
June 5	1.55	9	2.62
6	1.08	17	1.35
15	1.36	24	1.90
23	2.11	29	1.70
30	2.11	June 2	2.18
July 7	1.28	8	2.64
15	2.65	16	5.60
22	4.53	21	8.16
29	2.91	24	6.62
Aug. 5	3.72	July 3	14.80
12	3.49	6	24.40
24	2.58	11	24.46
29	1.31	17	23.13
Sept. 1	0.87	24	11.45
		31	9.96
		Aug. 5	10.56
		10	19.45
		17	16.25
		26	5.25
		30	3.65
		Sept. 9	0.50

of the flora of the lake it seems unlikely that the later copepod stages are herbivorous.

As stomach analysis yielded undigested portions of animals, six groups of animals which were abundant in the lake were selected as potential prey and fed, one or two groups at a time, to the *C. b. thomasi* copepodids IV and V and adults.

In experiments involving *C. b. thomasi* nauplii I–V as the food (Fig. 3*a*), the predation rate reached a maximum of 1.8 prey per predator, at a prey concentration of about 300 prey per litre. At prey concentrations greater than this, the number of prey eaten remained relatively constant, apparently at the maximum a predator could eat in 1 day.

When *C. b. thomasi* copepodids I–III were used as prey (Fig. 3*b*), the predation rate increased with increased concentration up to about 0.7 prey per predator per day, at concentrations of about 300 copepodids per liter of water.

When *Diaptomus oregonensis* and a few *Diaptomus hesperus* nauplii I–VI were used as prey (Fig. 3*c*), the predation rate increased up to about 1.6 prey per predator per day, at a prey concentration of 307 nauplii per liter, but beyond this concentration fewer prey were eaten.

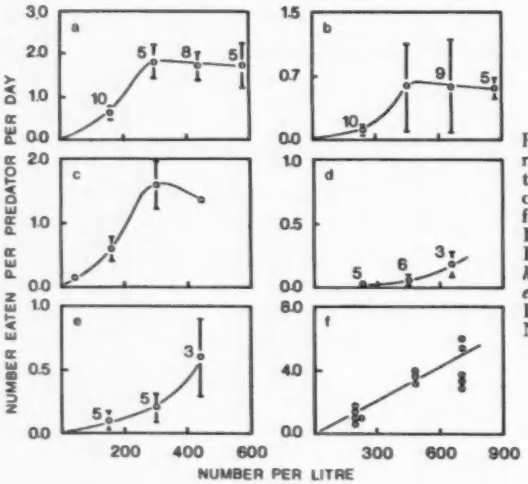

FIG. 3. Mean laboratory feeding rates (± one standard deviation of the sample mean) for *C. b. thomasi* copepodids IV and V and adults feeding on: (*a*) *C. b. thomasi* nauplii I–V; (*b*) *C. b. thomasi* copepodids I–III; (*c*) *D. oregonensis* and *D. hesperus* nauplii I–VI; (*d*) *D. oregonensis* and *D. hesperus* copepodids I–V; (*e*) Cladocera; and (*f*) rotifers. Numerals near the means are numbers of replicates.

When *Diaptomus oregonensis* and *D. hesperus* copepodids I–V were fed to the predator (Fig. 3*d*) few animals were removed. This was also the case when *Ceriodaphnia* sp. (Fig. 3*e*), an abundant cladoceran in Marion Lake, was used as prey. The average size of the members of both of these groups is equal to, or larger than that of the predator, and for this reason they may be less vulnerable as prey.

When cultures of *Keratella cochlearis* were used as prey, relatively high feeding rates were recorded (Fig. 3*f*) suggesting that these animals might be the preferred prey species.

When equal numbers of *Diaptomus* nauplii and *Ceriodaphnia* sp. were mixed at a total concentration of 306 organisms per liter, the mean number of *Diaptomus* nauplii eaten per predator per day in four replicates was 0.50 This compares favourably with the 0.56 nauplii eaten per predator per day when *Diaptomus* nauplii (Fig. 3*e*) were used alone at a concentration of 153 nauplii per liter. *Ceriodaphnia* sp. was eaten at the rate of 0.16 per predator per day, which is close to the 0.13 cladocerans eaten per predator per day when *Ceriodaphnia* sp. (Fig. 3*c*) was used alone at a concentration of 153 animals per liter. These data suggest that the predation rates obtained for single groups of prey might also be applicable to situations, like those in the lake, where prey are mixed.

Feeding Rates in the Lake

To further test the hypothesis that *C. b. thomasi* predators feed at the same rates on single and mixed groups of prey the predators were fed a mixture of prey at Marion Lake during the summer of 1968. At all times four predators and 20 prey were placed together in petri dishes which contained 50 ml of water. As the summer progressed the species composition of the 20 prey was varied as the species composition in the lake varied. Under these conditions predation rates were calculated for two prey groups: diaptomid and *C. b. thomasi* nauplii, and *K. cochlearis* rotifers.

The predation rates (prey per predator per day) for *D. oregonensis*, *D. hesperus*, and *C. b. thomasi* nauplii (Fig. 4) are very similar to those found in the laboratory (Fig. 3*a*, *c*). The predation rate increased as the concentration

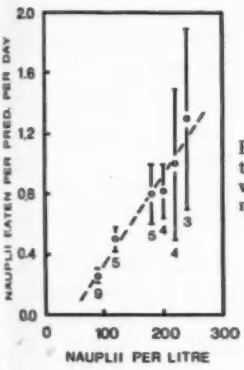

FIG. 4. Mean field feeding rates (± one standard deviation of the sample mean) for *C. b. thomasi* copepodids IV and V and adults when fed *C. b. thomasi*, *D. oregonensis*, and *D. hesperus* nauplii in a mixture of possible prey. Numerals near each mean are the numbers of replicates.

of nauplii increased. The predation rates obtained for *Keratella cochlearis* fed in a mixture of prey species in the field (the mixture included *K. cochlearis*, *D. oregonensis* nauplii, *D. hesperus* nauplii, and occasionally diaptomid copepodids), did not agree with the feeding rates determined in the laboratory (Fig. 3*f*). The following table summarizes the data obtained when *C. b. thomasi* copepodids IV and V and adults fed on *K. cochlearis* presented in a mixture of prey in Marion Lake.

No. of rotifers per liter	60	80	100	120	140	160	180	200	235
Prey per predator eaten per day	0.00	0.00	0.18	0.25	0.00	0.13	0.00	0.05	0.00
No. of replicates	3	5	4	2	2	2	2	5	5

The laboratory experiments suggested that *K. cochlearis* may be the preferred prey species whereas in the mixture used at the lake *K. cochlearis* was seldom eaten.

Standing Stock of Prey in the Lake

The predation rate studies in the laboratory or at the lake indicated that *Ceriodaphnia* sp. and *K. cochlearis* were seldom eaten by *C. b. thomasi* copepodids

IV and V and adults. These data suggest that in the lake, *C. b. thomasi* predators could not significantly reduce the standing stocks of these prey groups. The data on *C. b. thomasi* copepodids I–III, for the laboratory only, were insufficient to show whether or not *C. b. thomasi* predators could reduce the standing stock of the copepodids I–III.

The relatively high predation rates obtained for *C. b. thomasi* nauplii and diaptomid nauplii, both in the laboratory and at the lake, suggest that the standing stocks of these prey groups might be reduced by *C. b. thomasi* predators. The proportions of their standing stocks that might have been eaten was estimated by combining the predation rate with the data on the standing stocks of predators and prey.

The total proportion of a prey population that could have been eaten by *C. b. thomasi* predators during the summer of 1967 was calculated by dividing the number of prey that could be eaten (NEprey) by the number of prey that were recruited (NRprey) to the population. For *C. b. thomasi* nauplii I–V the number of prey eaten was estimated in the following manner:

$$\sum_{i=1}^{k} R_i \times Npred_i = NEprey \qquad (1)$$

where k is the number of days between May 19 and July 31, 1967, R_i is the rate of predation on the ith day (numbers per predator per day), $Npred_i$ is the concentration of predators found on the ith day (numbers per liter per day), and NEprey is the estimated number of prey eaten during the summer (numbers per liter per summer). The estimated number of nauplii eaten per liter (NEprey) for the period when the nauplii were present was 23.9 (Fig. 5*a*).

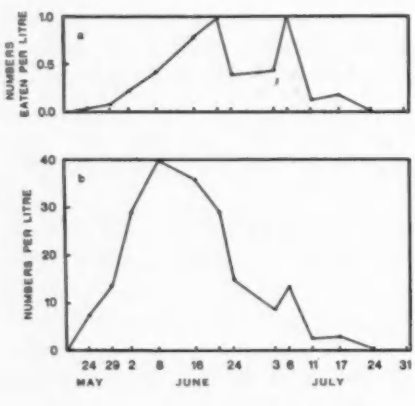

FIG. 5. (*a*) Estimated numbers of *C. b. thomasi* nauplii eaten by *C. b. thomasi* predators during the summer of 1967. (*b*) Standing stocks of *C. b. thomasi* nauplii during 1967.

The number of *C. b. thomasi* nauplii observed during the summer (Fig. 5*b*) was calculated from the expression:

$$\left(\sum_{i=1}^{k} \text{Nprey}_i\right)/rt = \text{NOprey} \tag{2}$$

where k is defined as in equation 1, Nprey_i is the concentration of prey observed on the ith day (Fig. 5*b*) (numbers per liter per day), rt is the residence time, which for *C. b. thomasi* nauplii averages 16 days, and NOprey is the number of prey present or observed during 1967 (numbers per liter per summer). The estimated number of observed prey (NOprey) for the period when the nauplii were present was 65.4.

The number of nauplii which survived the predation was estimated from:

$$\text{NSprey} = \text{NOprey} - \text{NEprey}/2 \tag{3}$$

where NSprey is the number of prey which were not eaten (number per liter per summer). The estimated number of surviving prey (NSprey) for the period when the nauplii were present was 53.4 (=65.4 − 23.9/2).

The number of prey eaten per liter per summer (NEprey, which was calculated in equation 1) may be written:

$$\text{NEprey} = \text{NRprey} \times u \tag{4}$$

where NRprey is the number of prey recruited to the population during 1967 (number per liter during the period they were present), and u is the proportion of the recruits that are eaten. The number of prey eaten (NEprey) may also be expressed as a proportion of the number surviving (NSprey), so that:

$$\alpha = \frac{\text{NEprey}}{\text{NSprey}} \tag{5}$$

and when equation 4 is substituted in 5, α may also be expressed as:

$$\alpha = \frac{\text{NRprey} \times u}{\text{NSprey}} \tag{6}.$$

For the period the nauplii were present, α equals 0.447 (=23.9/53.4).

The number of prey surviving predation (NSprey) may be written:

$$\text{NSprey} = \text{NRprey} \times (1-u) \tag{7}$$

and substituting equation 7 in 6:

$$\alpha = \frac{u}{1-u} \tag{8}.$$

Since $\alpha = 0.447$, $u = 0.31$; hence 31% of the total *C. b. thomasi* nauplius population recruited during the summer of 1967 could have been eaten by *C. b. thomasi* copepodids IV and V and adults.

These estimations may be partially checked by comparing NRprey (number of recruits per liter per summer) with the estimated number of nauplii I observed during 1967. From equation 7 NRprey = 76.6 (=53.4/(1−.447)) and 105.7 nauplii I were observed. This comparison indicates that the estimated predation mortality might account for about half of the total natural mortality experienced by the *C. b. thomasi* nauplius population.

The diaptomid nauplius population in Marion Lake was composed of about 95% *Diaptomus oregonensis* and 5% *D. hesperus*. During 1967 diaptomid nauplii were first caught on June 2. The standing stock increased to July 6, decreased until July 24, and remained low until August 26 (Fig. 6*b*). The estimated number of nauplii eaten per liter per summer (NEprey, calculated

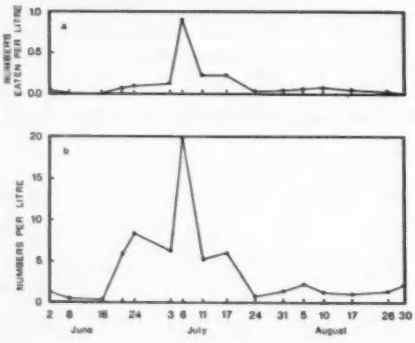

FIG. 6. (*a*) Estimated numbers of *D. oregonensis* and *D. hesperus* nauplii eaten by *C. b. thomasi* predators during the summer of 1967. (*b*) Standing stocks of the diaptomid nauplii during 1967.

from equation 1) was 19.2 (Fig. 6*a*). The total number of nauplii observed during 1967 (NOprey, calculated from equation 2 with $rt = 12$ days) was 53.8 per liter. The estimated number of nauplii surviving the predation (NSprey calculated from equation 3) was 44.2 (=53.8 − 19.2/2) per liter per summer. α (calculated from equation 4) was 0.435 (=19.2/44.2) and u (calculated from equation 7) was 0.302. Therefore, during the summer of 1967, an estimated 30.2% of the diaptomid nauplius population could have been eaten by *C. b. thomasi* copepodids IV and V and adults if these predators fed at the same rate while swimming free in the lake as they did during the feeding experiments.

For the diaptomid nauplii it was possible to check this estimate of the total predation with an estimate of the natural mortality arising from all causes experienced by the nauplius population during 1967. Laboratory experiments indicated that the eggs of *D. oregonensis* required 3 days to hatch at 18 ± 1 C. This temperature is close to the average summer temperatures of Marion Lake (Fig. 1). During 1967, 189.5 egg days were recorded (one egg per liter per day constitutes one egg day). Diaptomid copepodids I–V

had a mean residence time of about 20 days and 369.0 copepodid days were recorded. If there had been no mortality in the naupliar stages, 1263.3 (=20/3 × 189.5) copepodid days would be expected. These calculations indicate that the total natural mortality for diatomid nauplii was about 71% during 1967.

The suggestion that predation by *C. b. thomasi* may contribute significantly to the mortality of diaptomid nauplii is supported by two further pieces of evidence. As mentioned previously, the number of *C. b. thomasi* predators was lower in 1966 than in 1967 (Table 1). In view of this, the total mortality of nauplii should have been lower in 1966 than in 1967. During 1966 there were 128.5 egg days and 569.5 copepodid days and, therefore, a naupliar natural mortality of about 34%. This is lower than the corresponding estimate for 1967. Also, after August 26, 1967, when the number of *C. b. thomasi* predators was very low (Table 1) and the estimated daily predation dropped to near zero, the number of diaptomid nauplii increased from 1.45 per liter on August 26 to 2.20 per liter on August 30, 3.70 per liter on September 9, and 4.55 per liter on September 15. After September 15, 1967, it began to rain and most of the plankton were washed from the lake.

In the laboratory there was no predation on diaptomid copepodids at densities less than 100 per liter. During 1966 and 1967 the concentration in Marion Lake was never greater than 19 diaptomid copepodids per liter (Fig. 7).

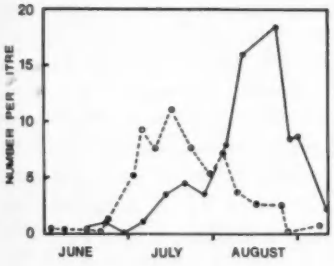

FIG. 7. Standing stocks of diaptomid copepodids I–V (*D. oregonensis* and a few *D. hesperus*) during 1966 (*solid line*) and 1967 (*broken line*).

This suggests that the predators could not have reduced the standing stocks of the diaptomid copepodid populations during either year.

DISCUSSION

In Marion Lake, during 1966 and 1967, the predatory population of *C. b. thomasi*, copepodids IV and V and adults, was divisible into two distinct groups. The first group was composed of those animals which excysted in the spring as stage IV copepodids. Their excystment was associated with a drop in the amount of water entering the lake and with a rise in temperature (Fig. 1). Smyly (1961, 1962) showed that after a long period in diapause, slight changes in temperature or turbulence were enough to cause *Cyclops*

leuckarti to break diapause. Deevey (1941) working on *Canthocamptus staphylinoides* and Cole (1953) working on *C. b. thomasi*, have reported similar occurrences. After their excystment in mid-April, the stage IV copepodids developed to adults, which began producing eggs.

It might be supposed that these animals would have to feed to build up energy for egg production; however, during 1967, none of the prey groups studied (Fig. 5, 6) was available from April 3 until May 24, and yet the main body of eggs was produced at the end of May. This might be explained by the fact that lipid droplets which occur in the body cavity of recently excysted cyclopoids (Birge and Juday, 1908; Elgmork, 1958, 1959) were also in the Marion Lake animals. These observations suggest that the copepodids of stage IV stored energy before going into diapause in the previous summer and that this energy maintained them throughout the winter in their encysted condition and also allowed the animals to excyst, moult twice, and produce eggs the following spring.

The first group of *C. b. thomasi* predators were still found in the plankton during June, when they were joined by the prey and by the second group of *C. b. thomasi* predators, composed of the newly moulted stage IV copepods. During June, July, and August of 1967, predation by both groups reduced the *C. b. thomasi* nauplius population by an estimated 30.0% and the diaptomid nauplius population by an estimated 30.2%.

During this period, however, the variation with time of the estimated predation for each prey group may have been influenced by three factors: temporal separation, vertical separation, and low prey density. The first two were discussed by Cole (1961, 1963) and Sandercock (1967) and appear to be important mechanisms for the coexistence of calanoid copepods. The third factor is of importance in planktonic predator–prey situations. The applicability of the three factors to the Marion Lake system is most clearly exemplified by the data collected during 1967, when physical conditions were relatively stable and the predator and prey populations developed in a situation free of violent climatic interference from outside the eco-system.

Temporal separation could have reduced predation between April 15, 1967, and May 29, 1967, when the predator population was composed of the few group-1 animals which excysted in April 1967, and died out during June 1967 (Fig. 2). Temporal separation (Fig. 8) also became important after August 26, when most of the group-2 predators had encysted. This case is most clearly exemplified by the diaptomid nauplius standing stock, which began to increase after August 26 (Fig. 6). Vertical separation (Fig. 8) reduced the possibility of predation on all of the prey from April 15 until about June 15. During this period the *C. b. thomasi* copepodids IV and V and adults were found almost exclusively in the top 2 m of water at all times, whereas the prey spent most of their time in the lower 2 m of the water column. Laboratory experiments indicated that for some prey groups, notably diaptomid copepodids, the percentage of the population that was eaten fell to zero below a critical prey density (Fig. 3). In the lake the diaptomid copepodids never

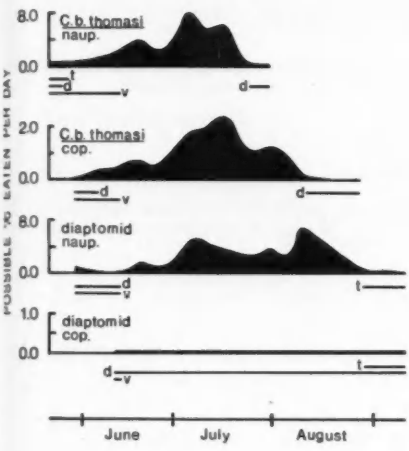

FIG. 8. Estimated daily predation by *C. b. thomasi* copepodids IV and V and adults on various prey. The periods during which the predators and prey were temporally or vertically separated are shown by lines marked "*t*" and "*v*." The lines marked "*d*" indicate the times at which the prey were so scarce that predation was undetectable.

exceeded a concentration of 19 copepodids per liter (Fig. 7) so that their estimated daily probability of being eaten was less than .01% (Fig. 8).

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Field Test of Fluorescent Pigment Marking and Finclipping of Coho Salmon[1]

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PHINNEY, DUANE E., AND STEPHEN B. MATHEWS. 1969. Field test of fluorescent pigment marking and finclipping of coho salmon. J. Fish. Res. Bd. Canada 26: 1619–1624.

Three lots of age 0 coho salmon were placed in a 6-acre dirt pond. Fish in one lot were marked with fluorescent pigment; those in a second lot were marked with a finclip; and those in a third lot were unmarked. Rainbow trout and age 1 coho were also placed in the pond as potential predators on the fry. After 6 months, sampling of the fry indicated that the fluorescent pigment lot survived and grew as well as the unmarked lot, but that the finclipped lot did not fare as well as the other two in terms of survival and growth.

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INTRODUCTION

A METHOD of using fluorescent pigment propelled by compressed air for marking fish for short-term population or behavioral studies was refined and tested by Phinney et al. (1967). They reported on the physical and chemical properties of the pigment, the application technique, and the results of hatchery tests with three species of age 0 salmon (*Oncorhynchus* spp.) and rainbow trout (*Salmo gairdneri*). They concluded that marking by this method is rapid and inexpensive, that the mark does not affect the survival of the fish, and that the mark is retained for at least 131 days.

Although the fluorescent pigment on a fish is discernible to the human eye only under ultraviolet light, fish so marked might be distinguished from unmarked ones and cropped selectively by their fish or bird predators. To test this possibility in a nearly natural environment containing predators, we conducted an experiment with age 0 coho salmon (*O. kisutch*) in Salmon Creek Pond, a man-made impoundment on a spring-fed tributary to Salmon

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Creek in southwestern Washington. The experiment was designed to compare growth and survival of fluorescent pigment-marked, finclipped, and unmarked fish.

METHODS AND MATERIALS

Salmon Creek Pond is 6 acres in surface area, averages 4 ft in depth, and has a bottom of mud and clay and a shoreline covered with dense vegetation. At the time of the experiment the predators commonly seen on the pond were kingfishers, mergansers, great blue herons, and aquatic garter snakes. Predation potential was increased by adding 192 age 1 coho salmon between 15 and 20 cm long and 29 rainbow trout between 21 and 36 cm long immediately before the pond was stocked with the age 0 coho. The only other fish in the pond were a few cottids (*Cottus* sp.).

The pond was stocked with three lots of age 0 coho. Fish in lot 1 were marked at 120 psi with red granule-size fluorescent pigment, fish in lot 2 were marked by removing the posterior half of the right maxillary bone and the left ventral fin, and fish in lot 3 were unmarked (Table 1). The air pressure used for the fluorescent pigment markings is within the range that produced satisfactory results for Phinney et al. (1967). The maxillary bone was chosen for the other marked group because it is often used in marked-fish experiments, but its effect on growth and survival has not been well documented. The maxillary bone mark is usually used in combination with one of the fins; we chose the left ventral fin because the ventral fin is easy to excise and does not regenerate often.

The coho came from a Washington Department of Fisheries hatchery on the Grays River, a lower Columbia River tributary. When they were 4 months old and averaged about 63 mm in fork length, about 15,000 were seined from one of the hatchery ponds and divided randomly into the three approximately equal experimental lots. A three-pocket "pie" type sampler (Hewitt and Burrows, 1948) was used for this separation to ensure similar size distribution among the three lots. The mean lengths of systematic samples of about 175 fish from each lot (Table 1) did not differ significantly from one another ($F = 0.08$; $df = 2, 524$). The control lot was handled like the one receiving fluorescent pigment, except that the marking gun delivered air without the pigment. The fish were marked and counted on May 26, 1967, and held for 1 week at the hatchery so that deaths due to handling could be determined (Table 1). The fish were mixed together in the planting truck at the end of the holding period and transported the 100 miles to Salmon Creek Pond.

A random sample of 100 fish from lot 1 was inspected before transporting to Salmon Creek Pond and 98 were found to have retained the dye. Therefore, 2% of the survivors of lot 1 (column 5, Table 1) was subtracted from that lot and added to lot 3 for an estimate of the numbers of marked and unmarked fish actually planted.

RESULTS AND DISCUSSION

On November 16, nearly 6 months after stocking, samples were taken with three hauls of a 100-ft, ½-inch mesh beach seine and a variable-mesh gillnet (½–1½ inches) set for 36 hr (2 nights and 1 day). The combined samples contained 695 age 0 coho and there was no significant difference in the proportions in each experimental lot by method of capture ($\chi^2 = 0.088$; $df = 2$) or in mean length by method of capture ($F = 0.13$; $df = 1, 689$[a]) (Table 2). Therefore, the two sampling methods for purposes of the experiment were

[a]One fish in lot 1 (taken by gillnet) and three fish in lot 3 (taken by gillnet) could not be measured accurately because of frayed caudal fins.

TABLE 1. Number and mean fork length of age 0 coho

TABLE 1. Number and mean fork length of age 0 coho salmon in each of three lots at the beginning of the experiment in Salmon Creek Pond.

Exptl. lot	Original lot size (*no.*)	Mean length (*mm*)	Deaths during 1st week		Survivors (*no.*)	Lot size after adjustment for nonretention of dye	
			No.	%		No.	Proportion
1. Fluorescent pigment-marked	5,713	63.00	98	1.72	5,615	5,503	0.383
2. Finclipped	4,214	62.43	57	1.35	4,157	4,157	.289
3. Control	4,718	62.62	107	2.27	4,611	4,723	.328
Total	14,645	62.71	262	1.78	14,383	14,383	1.000

TABLE 2. Number, mean fork length, and proportion of age 0 coho salmon in each of three experimental lots in the samples taken from Salmon Creek Pond on November 16.

Exptl. lot	Method of capture								
	Gillnet			Beach seine			Combined		
	No.	Mean length (*mm*)	Proportion	No.	Mean length (*mm*)	Proportion	No.	Mean length (*mm*)	Proportion
1. Fluorescent pigment-marked	217	124.11	.400	62	124.35	.408	279	124.16	.401
2. Finclipped	133	122.24	.245	38	122.58	.250	171	122.32	.246
3. Control	193	124.04	.355	52	124.25	.342	245	124.08	.353
Total	543	123.62	1.000	152	123.87	1.000	695	123.67	1.000

considered equivalent, and the totals were used for comparison with the initial population.

The initial composition of the population is compared with the composition of the November 16 sample in Table 3. The hypothesis that the relative composition of the total population of coho was the same after 6 months as when planted was rejected at the .05% level of significance ($\chi^2 = 6.31$; df = 2). Inspection of Table 3 reveals that the significant χ^2 value was due to a less than expected number of finclipped fish in the sample (under the null hypothesis

TABLE 3. Comparison of initial and terminal population composition.

Exptl. lot	Initial size (*no.*)	Initial proportion	Nov. 16 sample size		Expected sample composition under hypothesis of no change in composition
			No.	Proportion	
1. Fluorescent pigment-marked	5,503	.383	279	.401	266
2. Finclipped	4,157	.289	171	.246	201
3. Control	4,723	.328	245	.353	228
Total	14,383	1.000	695	1.000	695

of no change in population composition). Comparing only the fluorescent pigment-marked and control fish the sample proportions were not significantly different from the initial proportions of fish in these two categories ($\chi^2 = 0.07$; df = 1). A similar test comparing only the finclipped and control lots yielded a highly significant χ^2 value ($\chi^2 = 5.43$; df = 1; $P = 0.02$). Therefore, it was concluded that the rate of survival was equal for the fluorescent pigment-marked and control lots but less for the finclipped lot than for the other two.

Although the actual survival rates could not be determined with these data, it was estimated that the survival rate of the control and fluorescent pigment-marked lots was 1.25 times greater than the survival rate of the finclipped lot.

Let s_1 = rate of survival for the fluorescent pigment-marked and control lots; s_2 = rate of survival for the finclipped lot; N_1 = initial number of fluorescent pigment-marked and control fish; N_2 = initial number of finclipped fish; n_1 = sample number of fluorescent pigment-marked and control fish; n_2 = sample number of finclipped fish; u = rate of capture (assumed equal for the three lots). Then $n_1 = N_1 s_1 u$; $n_2 = N_2 s_2 u$. Therefore

$$s_1 = \frac{N_2}{N_1} \cdot \frac{n_1}{n_2} \cdot s_2 = \frac{4,157}{10,226} \cdot \frac{524}{171} \cdot s_2 = 1.25\, s_2.$$

The possibility exists that the presence of the finclipped fish may have modified the results of the comparison of relative survival rates between the fluorescent-pigment and control lots. For if the predators had selected finclipped fish to the exclusion of the other two groups this also would have produced the result of no difference in survival rate between the fluorescent-pigment and control lots. However, it seems highly unlikely that the finclipped fish would be selected to the exclusion of the other two groups and, if there was any significant amount of predation on these two groups, which seems certain, the conclusion regarding their relative survival rates is still valid. Moreover, there is no reason to assume that all of the mortality was the result of predation. Again, supposing the predators had selected finclipped fish to the exclusion of the other two groups, the conclusion would still hold that the total mortality resulting from all other factors was equal for the two fluorescent pigment-marked and control lots.

A potential source of error was loss of marks during the course of the experiment. For neither type of mark, however, was this thought to be significant. No fish in the November 16 sample had only a ventral or only a maxillary mark, and the probability of regeneration of both the ventral fin and the maxillary bone is very low. For example, Worlund et al. (1969) found rates of regeneration of the ventral fin (wherein 25% or more of the fin had grown back) ranging from 3.7 to 6.0% in several lots of fall chinook salmon (*O. tshawytscha*) representing 4 brood years, which were marked at age 0 and held in a hatchery for 2 years. Regeneration rates for the maxillary bone (removed to a point intersecting a vertical line through the midpoint of the eye, as done in our experiment) ranged from 0.5 to 3.4% for similar experiments by the same authors. The fluorescent pigment was found to endure with only 2% loss for 6 months on chinook salmon (*O. tshawytscha*) (Denny M. Miller, personal communication). Additionally, Arthur E. Newell found no loss of marks after 6 months on Atlantic salmon (*S. salar*) (personal communication). Indirect evidence from our experiment also suggests that loss of either type of mark was not a significant factor. Fish of either marked lot losing its mark would be considered a control fish when captured. The control lot, however, did not increase relative to the fluorescent pigment-marked lot. If there had been a mark loss, there would have to have been a higher mortality in the control lot than in the fluorescent pigment-marked lot to produce the unchanged relative abundance. This is an unlikely event.

An analysis of mean lengths of the samples indicated that fluorescent pigment-marking had no detrimental effects on growth, whereas finclipping did (Table 2). The hypothesis of equal mean lengths at the time of capture was rejected at the .05 level of significance ($F = 4.45$; $df = 2, 688$). Scheffé's (1953) test at the .10 level indicated that there was no difference in mean length between the fluorescent pigment-marked lot and the control lot but that the mean length of the finclipped lot was less than the mean length of either of the other two lots.

In summary, fluorescent pigment-marking had no apparent ill effect on either rate of survival or growth over a 6-month period in a relatively natural environment, whereas finclipping had detrimental effects on both. Whether differential predation was the cause for lower survival rate of the finclipped fish is not known.

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Optimal Extraction Conditions of Chlorophylls from Cultures of Five Species of Marine Phytoplankton[1]

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Considerable variation was found in the success of extraction of chlorophyll pigment from different species of phytoplankton by grinding. The optimal conditions for chlorophyll *a* were established for *Dunaliella tertiolecta*, *Thalassiosira nordenskioldii*, *Chaetoceros curvisetus*, *Fragilaria* sp., and *Phaeodactylum tricornutum*. Significant conclusions could not be drawn for chlorophyll *c* because of the relative imprecision of the chlorophyll *c* measurement compared with chlorophyll *a*. For chlorophyll *a*, ease of extraction was inversely related to the dry weight:chlorophyll *a* ratio.

Subba Rao, D. V., and T. Platt. 1969. Optimal extraction conditions of chlorophylls from cultures of five species of marine phytoplankton. J. Fish. Res. Bd. Canada 26: 1625–1630.

L'utilisation d'un homogénéiseur pour l'extraction de la chlorophylle *a* donne des résultats très variables selon les différentes espèces de phytoplankton. Pour *Dunaliella tertiolecta*, *Thalassiosira nordenskioldii*, *Chaetoceros curvisetus*, *Fragilaria* sp. et *Phaeodactylum tricornutum*, on a établi les conditions optimales pour l'extraction de la chlorophylle *a*. Pour la chlorophylle *c* on n'a pas pu tirer de conclusions significatives parce que la précision de la mesure de la chlorophylle *c* est moindre que celle de la chlorophylle *a*. Pour la chlorophylle *a*, le succès de l'extraction est en raison inverse due rapport poids sec:chlorophylle *a*.

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INTRODUCTION

Chlorophyll concentrations are widely used for the estimation of both phytoplankton biomass and photosynthetic rate. In general, extraction of pigments by grinding the cells gives higher chlorophyll values than when the cells are not ground. Complete extraction of photosynthetic pigments can be achieved only by a suitable combination of grinding time, extraction time, and extraction temperature, and for any given species, the optimal conditions of pigment extraction by grinding are generally unknown.

The importance of using optimal extraction procedure should not be underestimated. Much work is now being done using cultures of marine phytoplankton to elucidate the response of photosynthetic systems to environmental factors and is the subject of considerable controversy (Yentsch and Lee, 1966; Steemann Nielsen and Jørgensen, 1968). Optimal extraction conditions become

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critical when chlorophyll concentration is used as a reference unit to describe the physiological response of phytoplankton.

We report here the results of grinding and extraction procedures for the chlorophylls in cultures of *Dunaliella tertiolecta*, *Thalassiosira nordenskioldii*, *Chaetoceros curvisetus*, *Fragilaria* sp., and *Phaeodactylum tricornutum*. Optimal combinations for the determination of pigments appear to differ significantly among the species.

MATERIALS AND METHODS

The phytoplankters employed in this study were isolated from Nova Scotian shelf waters and grown for 4 days in an artificial medium (Humphrey and Subba Rao, 1967) at 1.27×10^5 ergs/cm^2 sec continuous light and 10 C. Cultures (25 ml) of each of *D. tertiolecta* and *P. tricornutum* were diluted to 1000 ml with filtered sea water prior to grinding. For the other phytoplankters, which have relatively less chlorophyll per cell, 40-ml cultures were diluted to 1000 ml. Subsamples of 100 ml were used for pigment analysis. The chlorophyll concentrations in the subsamples were similar to those reported from Nova Scotian shelf waters (Platt and Irwin, MS, 1968). The results will therefore be applicable to local field conditions.

Chemical analysis was the same as described by Kerr and Subba Rao (1966). A Millipore filter (HA 0.45 μ, white, plain, 47 mm) was placed in a Millipore filter holder and covered with about 0.1 g $MgCO_3$. About 50 ml of filtered sea water was added and sucked through to spread the $MgCO_3$. The 100 ml of the phytoplankton subsample was added and filtered applying a suction of 5 inches. The sides of the funnel were washed with filtered sea water. After filtration, the filter was folded and pushed to the bottom of the homogenizer as described by Humphrey and Wootton (1966). Three ml of 90% acetone were added and the filter was ground for a specific duration using the pestle at 500 rpm. The contents of the homogenizer were poured into a Nalgene centrifuge tube. The homogenizer and pestle were washed twice with 5 ml of 90% acetone and the washings were added to the Nalgene tube. The tube was stoppered with a Nalgene stopper and kept dark at the required temperature for a specific period. The extract was then centrifuged at 4300 *g* for 10 min in an angle centrifuge. The supernatent liquid was poured into a 15-ml centrifuge tube graduated in units of 0.1 ml, and diluted to 10 ml with 90% acetone. Extinctions were read at 750, 663, 645, and 630 mμ against a 90% acetone blank in a 1-cm cell in a Beckman DU Spectrophotometer. Turbidity corrections were made by subtracting the extinction at 750 mμ from the extinctions at the other wavelengths. Because the algal cultures in this study contained only chlorophyll *a* and *c* or *a* and *b*, the following two component equations developed by Humphrey and Jeffrey (unpublished data) were used to calculate the chlorophylls:

$$\text{Chl } a = 13.31_{e663} - 0.27_{e630}$$
$$\text{Chl } c = -8.37_{e663} + 51.72_{e630}$$

or

$$\text{Chl } a = 13.50_{e663} - 2.91_{e645}$$
$$\text{Chl } b = -4.33_{e663} + 21.20_{e645}$$

For each species the chlorophyll was determined at three temperatures (0, 20, 40 C) grinding times (30, 90, 270 sec), and extraction times (10, 75, 375 min) in a $3 \times 3 \times 3$ factorial design, that is, 27 experiments were run on each species. These could not be handled simultaneously; it was therefore convenient to divide each series into three blocks of nine samples prepared under uniform conditions from the same stock culture. Since the stock cultures of any species did not have identical cell densities, significant differences between the blocks were anticipated. The main effects and two-factor interactions were freed from the influence of the variations between blocks by confounding a pair of three-factor interactions as described by Davies (1963, p. 438). To the extent that the mean square due to blocks would be high relative to the error term, the

precision of the analysis would be increased by the confounding procedure, compared to a design in which the 27 treatments were allocated randomly to the blocks.

RESULTS

The results of the three-factorial analyses of variance are summarized in Table 1.

CHLOROPHYLL *a*

For *D. tertiolecta* and *T. nordenskioldii* no significant difference between the 27 treatments was detected (Table 1A and B).

In *C. curvisetus* (Table 1C) the effect of temperature was possibly significant. The mean values, averaged over all treatments, were 0.49 μg chlorophyll *a*/liter at 0 C, 0.48 at 20 C, and 0.41 at 40 C.

In *Fragilaria* sp. (Table 1D) the effect of extraction time was significant. The mean values averaged over all treatments, for the different extraction times were 0.41 μg *a*/liter at 10 min, 0.44 at 75 min, and 0.49 at 375 min. The effect of grinding time was possibly significant; the mean values were 0.46 μg *a*/liter at 30 sec, 0.41 at 90 sec, and 0.46 at 270 sec. The two-way table for grinding and extraction, averaged over all temperatures, is given below:

		Grinding time (*sec*)		
		30	90	270
		Chlorophyll *a* μg/liter		
Extraction time (*min*)	10	0.42	0.35	0.44
	75	0.47	0.38	0.46
	375	0.49	0.50	0.49

The highest yield was achieved by a combination of 90 sec grinding and 375 min extraction, but there was little difference between the effects of the three grinding times for 375 min extraction.

In *P. tricornutum* (Table 1E) the effects of grinding time and extraction were both significant, as was the interaction of these two. The mean values for the different grinding times, averaged over all treatments, were 0.56 μg *a*/liter at 30 sec, 0.61 at 90 sec, and 0.69 at 270 sec. The mean values for the different extraction times were 0.58 μg *a*/liter at 10 min, 0.66 at 75 min, and 0.60 at 375 min. The two-way table for grinding and extraction times, averaged over all temperatures, is given below:

		Grinding time (*sec*)		
		30	90	270
		Chlorophyll a μg/liter		
Extraction time (*min*)	10	0.52	0.61	0.62
	75	0.59	0.59	0.80
	375	0.57	0.62	0.59

This table shows that the highest yield was obtained using a combination of 270 sec grinding and 75 min extraction. The yield decreased sharply for any other combination.

TABLE 1. 3 × 3 × 3 factorial analyses of variance tables.

Source	df	Chlorophyll *a*			Chlorophyll *c* or *b*[b]		
		Mean square	F	Significance[a]	Mean square	F	Significance[a]
		A. *Dunaliella tertiolecta*[b]					
T	2	0.0173	<1	NS	0.0433	<1	NS
G	2	0.0425	<1	NS	0.0471	<1	NS
E	2	0.3750	2.95	NS	0.1311	<1	NS
T×G	4	0.1914	1.50	NS	0.1258	<1	NS
T×E	4	0.0760	<1	NS	0.0963	<1	NS
G×E	4	0.0407	<1	NS	0.0438	<1	NS
Blocks	2	38.4118	3.02	HS	0.7676	3.02	HS
Error	6	0.1274			0.2483		
		B. *Thalassiosira nordenskioldii*					
T	2	0.0041	<1	NS	0.1878	<1	NS
G	2	0.0109	1.53	NS	0.0937	<1	NS
E	2	0.0047	<1	NS	0.1393	<1	NS
T×G	4	0.0181	2.54	NS	0.0728	<1	NS
T×E	4	0.0164	2.31	NS	0.1620	<1	NS
G×E	4	0.0184	2.59	NS	0.1193	<1	NS
Blocks	2	0.7524	105.80	HS	0.2162	1.14	NS
Error	6	0.0071			0.1885		
		C. *Chaetoceros curvisetus*					
T	2	0.3504	4.94	PS	0.0183	<1	NS
G	2	0.0691	<1	NS	0.2137	1.63	NS
E	2	0.0341	<1	NS	0.3720	2.83	NS
T×G	4	0.0394	<1	NS	0.0447	<1	NS
T×E	4	0.0883	1.24	NS	0.1994	1.51	NS
G×E	4	0.0552	<1	NS	0.0934	<1	NS
Blocks	2	0.9216	13.01	HS	0.1209	<1	NS
Error	6	0.0709			0.1317		
		D. *Fragilaria* sp.					
T	2	0.0512	<1	NS	0.0214	<1	NS
G	2	0.1982	3.83	PS	0.5648	2.75	NS
E	2	0.4001	7.74	S	0.1776	<1	NS
T×G	4	0.0847	1.64	NS	0.0782	<1	NS
T×E	4	0.1262	2.44	NS	0.0997	<1	NS
G×E	4	0.0731	1.41	NS	0.0595	<1	NS
Blocks	2	3.7772	72.70	H S	0.6764	3.29	PS
Error	6	0.0518			0.2052		
		E. *Phaeodactylum tricornutum*					
T	2	0.0968	1.27	NS	0.0972	2.71	NS
G	2	0.6346	8.38	S	0.0158	0.44	NS
E	2	0.3860	5.10	S	0.1299	3.60	PS
T×G	4	0.0911	1.20	NS	0.1260	3.51	PS
T×E	4	0.1075	1.41	NS	0.0828	2.29	NS
G×E	4	0.3471	4.58	S	0.1021	2.84	NS
Blocks	2	5.0026	66.4	HS	0.1559	4.33	PS
Error	G	0.0758			0.0359		

[a]HS = highly significant: $P \leq 1\%$; S = significant: $1\% < P \leq 5\%$; PS = possibly significant: $5\% < P \leq 10\%$; NS = not significant.
[b]Chlorophyll *b*.

CHLOROPHYLL *c*

No significant effect on the chlorophyll *c* measurement was detected between the 27 different combinations of grinding time, extraction time, and extraction temperature, although the chlorophyll *c* measurements were made on the same extracts as were those for chlorophyll *a*. To test whether the lack of significance arose from the lower precision of single chlorophyll *c* determinations, a two-level analysis of variance of the results was made, so that the relative magnitudes of the standard deviations within the blocks for the two chlorophyll components could be estimated (Table 2). The ratio of the standard

TABLE 2. Comparison of the variability within blocks for chlorophyll *a* and *c* or *b*.[a]

Phytoplankter	Chlorophyll *a*			Chlorophyll *c* or *b*[b]		
	$\bar{x}$	σ_o	$\frac{\sigma_o}{\bar{x}} \times 100$	$\bar{x}$	σ_o	$\frac{\sigma_o}{\bar{x}} \times 100$
Dunaliella tertiolecta	6.9743	1.1618	24	1.3080[b]	1.6149	123
Thalassiosira nordenskioldii	1.8639	0.5420	29	0.7027	1.8411	262
Chaetoceros curvisetus	2.2850	1.4367	63	1.0250	1.8297	179
Fragilaria sp.	2.2191	1.6572	75	1.0856	1.9256	177
Phaeodactylum tricornutum	3.0637	2.2072	72	1.0549	1.3944	132

[a] σ_o is the standard deviation within blocks (24 df); $\bar{x}$ is the grand mean over the three blocks (27 observations).

[b] Chlorophyll *b*.

deviation within the blocks (σ_o) to the grand mean of the three blocks ($\bar{x}$) is taken as a measure of the relative precision of the chlorophyll measurement. For chlorophyll *a* the ratio of 100 $\sigma_o : \bar{x}$ was not greater than 75% for any species, whereas for chlorophyll *c* or *b*, this ratio was not less than 123% for any of the five species studied.

DISCUSSION AND CONCLUSIONS

The relative variability within the blocks was much higher for chlorophyll *c* than for chlorophyll *a* (Table 2). The lack of significance for chlorophyll *c* in the results of the factorial analyses was probably due to the relative imprecision of the chlorophyll *c* measurement, which masks the effects of differences between treatments. Richards with Thompson (1952) and Humphrey and Wootton (1966) found the coefficient of variation of chlorophyll *c* analysis to be about three times higher than that for chlorophyll *a*. Richards with Thompson (1952) and Madgwick (1966) attributed this error to the small absorption of chlorophyll *c* in the red end of the spectrum.

Table 3 summarizes the optimal conditions for the extraction of pigments from each of the five species of phytoplankton. In those instances where a

TABLE 3. Optimal conditions for extraction of pigments in five species of marine phytoplankton with corresponding dry weight per unit chlorophyll *a*.

Phytoplankter	Temp (*C*)	Grinding time (*sec*)	Extraction time (*min*)	$\frac{\mu g \text{ dry wt}^a}{\mu g \text{ chl } a}$
Dunaliella tertiolecta	20	30	10	69–130
Thalassiosira nordenskioldii	20	30	10	84–110
Chaetoceros curvisetus	0	30	10	72–148
Fragilaria sp.	20	90	375	92–188
Haeodactylum tricornutum	20	270	75	124–275

[a]Values indicate the range between different samples.

significant effect was not noticed we have recommended the most convenient conditions; these will suffice until a different set of conditions is shown to be preferred.

In Table 3, the five species are arranged in an order which reflects the relative ease with which the pigments may be extracted from the cells. Table 3 also gives the ratios of dry weight:chlorophyll *a*. In general, we conclude that the heavier the cell per unit chlorophyll *a*, the more difficult it is to extract the pigment. The only other species studied in detail, *Nitzschia closterium*, fits into this generalisation; it has a dry weight : chlorophyll *a* ratio of 80 (Madgwick, 1966) and the optimal extraction conditions found by Kerr and Subba Rao (1966) were 30 sec grinding and 10 min extraction at room temperature.

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Growth of Juvenile Chum Salmon (*Oncorhynchus keta*) Under Different Feeding Regimes

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Juvenile chum salmon were fed on six different concentrations of size-selected zooplankton for 8 weeks. Zooplankton were caught daily and sorted through sieves into size-groups roughly as follows: 6–20 mm total length, mainly euphausiids; 2.5–4.5 mm, mainly copepods; and ≤1.5 mm, mainly small copepods. The rate of growth in weight of the fish was found to be dependent upon the concentration of the ration. Fish which were offered no food lost weight, and fish which were offered excess food increased in weight by 5.4% per day. The mean growth rate of the fish held on fixed rations ranged from 2.2 to 5.7% per day and was found to be independent of the type of prey. Electivity experiments showed that all the fish selected copepods 1.6–4.5 mm long in proportion to their abundance and rejected copepods ≤1.5 mm. The euphausiids were selected only by fish which had previously fed on euphausiids. The effect of variations in the availability of prey is discussed.

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INTRODUCTION

In a recent article, Paloheimo and Dickie (1966) developed an equation for the dependence of the growth of fish on their food intake. Inferred from this equation is the suggestion that the exponent governing the relationship between growth and food depends on how much energy is expended by an organism in searching for, and capturing, different prey. Similar conclusions have been reached by Warren and Davis (1966), Mann (1966), and Kerr and Martin (1968). Kerr and Martin, in studying the food chain of trout, suggest that the potential increase in ecological efficiency which might be expected from a short food chain is counteracted by the fact that short food chains may produce a type of prey which is less efficiently captured by fish than that produced by longer food chains. In view of the above conclusions it would appear logical to test the effect of different types of prey as food for juvenile fish.

In earlier studies (Parsons and LeBrasseur, 1968), the importance of prey size and type in relationships between zooplankton and phytoplankton, and between fish and zooplankton, were discussed. In the latter relationship it was shown that during short-term (2-hr) feeding experiments, juvenile salmon feed most efficiently (as measured by the quantity of prey captured) on *Calanus plumchrus*, less efficiently on *Euphausia pacifica*, and poorly on

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Pseudocalanus minutus. However, as emphasized at the time, these short-term experiments did not show how the searching and capturing of a prey might affect the growth of the fish, nor was it established whether the choice of prey was related to the previous feeding history of the fish. In the following study the searching for prey was minimized and the effect of prey size alone was investigated by feeding various concentrations of three different natural prey to young salmon over a period of 8 weeks, during which a good measure of their growth could be obtained.

The studies were carried out at Saanich Inlet, B.C., during the period May 14 to July 12, 1968. Previous experience indicated that juvenile pink or chum salmon (*Oncorhynchus gorbuscha* Walbaum and *O. keta* Walbaum) would be suitable as predators and that crustacean zooplankton, *Pseudocalanus minutus* (Krøyer), *Calanus plumchrus* Marukawa, and *Euphausia pacifica* Hansen, are suitable prey. Both the prey and the predators were known to exist naturally together in the inlet during the experimental period.

METHODS

Laboratory-reared juvenile chum salmon from the Biological Station, Nanaimo, B.C., were used as the experimental animal. All fish had less than 2 weeks' feeding on hatchery foods prior to being transferred to the experimental tanks at Saanich Inlet. At the time the chum salmon were placed in the experimental tanks they measured on the average 41 mm in fork length (range 37–44 mm) and had an average weight of 0.45 g. Approximately 200 chum were placed in each tank, giving a total of about 90 g of fish per tank. The actual number per tank was not determined until near the end of the experiment, when the number of fish could be reliably counted and the total was obtained as the sum of the number remaining and the number already sampled (including any fish that had died).

The basic experimental unit consisted of three sets of six dark green Fiberglas tanks each containing $\frac{1}{4}$ m^3 sea water. One set of tanks was used for each of the three preys which were offered at six different concentrations. One additional tank held fish which were offered no food and another tank held fish which were offered excess food. Short-term electivity experiments were carried out in another set of 6 tanks.

The entire array of tanks was mounted on a barge floating in Saanich Inlet. A white translucent cover over the barge permitted the passage of light but prevented excessive heating of the tanks, and also prevented passing overhead objects from disturbing the fish. Each tank was fitted with a plywood lid covering two-thirds of the tank to provide a range of light intensities and cover for the fish.

A continuous supply of sea water was pumped into each bank of tanks from 2 m depth using two $\frac{3}{4}$ hp pumps. These pumps provided 3 liters of water per minute to each tank. The water was jetted into each tank, producing a current along the sides of the tank, and discharged through a central standpipe. Initial attempts at filtering all microfauna from the water proved impractical; coarse mesh screens over the intake funnels prevented large (>2 mm) organisms from entering the system. Provision was made for aerating the water, but this was found to be unnecessary. The tanks were scrubbed and cleaned daily and the entire intake system was flushed with fresh water once a week. The water temperature in the tanks varied less than 1 degree C per day and ranged from 14 C in May to 16 C in mid-July.

Live zooplankton were collected each morning from Saanich Inlet using plankton nets. The catches were passed gently through a series of sieves by repeated washings to obtain size fractions of the plankton. Medusae, seaweed, and detrital material were removed. Organisms passing through a 1-cm mesh sieve and retained on 2 mm mesh formed the largest size fraction, 6–20 mm; *E. pacifica* predominated in this size group. Organisms passing 2 mm mesh and retained

on 1 mm mesh formed the second size group which mostly consisted of *C. plumchrus*, 2.5–4.5 mm in total length. The smallest size group, ≤1.5 mm, predominantly *P. minutus*, was obtained after the samples had passed through 0.5 mm mesh and were retained on 0.1 mm mesh. Organisms, predominantly *C. pacificus*, retained on the 0.5 mm mesh were discarded. The sieving treatment damaged and killed many organisms and each size group contained some smaller organisms as well as those being selected. Each group was retained in fresh sea water and taken to the laboratory where the wet weight of an aliquot of each of the groups was made to determine the amount collected.

The fresh zooplankton were then distributed in measured amounts by weight to the fish. The prey were added fresh daily to the tanks, the concentrations (in grams) ranging from approximately 3 in tank 1 through 6.6, 10, 13, and 16.5 in succession to 18.5 in tank 6 (Table 1).

The prey concentrations were added on the assumption that there were 90 g of fish in each tank. In practice this was not realized since there were not equal numbers of fish in the various tanks at the beginning of the experiment and the fish were continuously increasing in weight. Varying numbers of fish were sampled weekly by removal from each tank in an attempt to maintain the total weight of fish within a reasonable range, 80–100 g. In determining the ration per gram of fish it was necessary to calculate the mean total weight of fish in each tank each week, i.e., the mean of the total fish weight at the beginning of a week and the total fish weight at the end of the week. There may be up to a 17% variation in the weight of prey added daily to each tank. This variation in ration weight coupled with an increasing total weight of fish each week gives a computed daily ration per gram of fish which varies from tank to tank irrespective of the prey. The mean per cent ration, rounded to the nearest whole number, for the 8-week period for each tank is considered to be sufficiently precise for the purposes of this report.

Samples of fish randomly drawn from each tank were taken each week for wet weight and dry weight determinations and for stomach content analysis. For determining weights, the fish samples were drained in sieves and stored in plastic bags prior to freezing. The mean wet weight of fish in each tank (Table 2) was determined by dividing the total wet weight of the fish sampled by the number of fish sampled per tank. The samples were then frozen and subsequently the freeze-dried weight was determined. For analyzing stomach contents, samples were taken after the fish had been feeding 2 hr and were preserved in formalin. The biomass (wet weight) of the prey per stomach was estimated from length–weight graphs for the various prey, and the organisms in the different length categories in the stomachs were counted. Fulton (MS, 1968) provides examples of length–weight graphs for some zooplankton. The data on mean wet weights were subjected to regression analysis with the criterion that a straight line be drawn through the respective points. The initial numerical analyses involved a logarithmic transformation of the weight data. All regression lines were found to be highly correlated with the observed data. The data were degraded by the regression to the extent that the weight of fish in the initial 2 weeks was underestimated whereas in the last 2 weeks it was overestimated. However, it is the overall effect of feeding on various sizes of prey as manifested by growth in weight over a critical period of the fish's life which was being examined; consequently, the variations from a straight line were not considered as relevant to the problem since each group of fish was treated alike. It is to be noted that the growth in weight computed from the observed data in Table 2 would be lower than the values reported in Table 3 which were calculated from the regression. The advantage offered by the drawing of straight lines through the data was that it permitted the calculation of an average rate of growth for fish in each tank. The growth rate was expressed as per cent increase in wet weight per day.

Once each week, samples of the rations were taken to determine the respective species and size compositions and the nitrogen and carbon contents. The micro-Pregl and the micro-Dumas methods, as modified by the use of Coleman Semi-Automatic Analyzers (Strickland and Parsons, 1968) were used for the measurements of total carbon and total nitrogen respectively (Table 4). No significant differences were found in carbon or nitrogen content with respect to the kind of prey. Apparently the nutritive values for the various prey were similar over the 8-week period.

TABLE 1. Daily rations (as percentages of fish weights)[a] of juvenile chum for various weeks for each of three kinds of prey. Numbers of salmon in tanks are given in parentheses.

	Daily ration (g)					
Week	3.3	6.6	13.2	10.0	16.5	18.5
	Prey mainly *Euphausia pacifica*					
1	3.0(214)	5.1(221)	6.4(172)	10.2(215)	10.4(204)	15.5(190)
2	3.3(164)	6.3(141)	9.2(127)	9.4(165)	13.6(134)	16.5(120)
3	3.4(144)	7.0(121)	9.0(108)	10.8(120)	15.7(91)	17.2(90)
4	2.9(134)	5.9(111)	6.5(98)	9.2(95)	13.9(71)	15.0(70)
5	3.4(94)	5.8(82)	8.3(58)	11.0(55)	16.5(41)	14.2(45)
6	3.2(84)	6.2(55)	8.6(43)	12.6(35)	15.1(36)	16.2(25)
7	3.3(74)	6.7(45)	8.9(33)	13.9(25)	15.9(26)	21.5(15)
8	4.0(64)	7.2(40)	9.6(23)	14.0(20)	15.9(18)	17.9(15)
Mean	3.3	6.2	8.3	11.3	14.0	16.7
	Prey mainly *Calanus plumchrus*					
1[b]	(2.0)(184)	(3.6)(192)	(4.9)(202)	(6.4)(202)	(7.6)(201)	(10.0)(182)
2	3.7(164)	6.8(162)	10.1(167)	13.6(142)	16.8(131)	20.3(112)
3	3.7(144)	6.0(142)	8.9(137)	12.3(112)	16.5(96)	15.6(92)
4	2.9(134)	5.3(112)	7.7(102)	11.6(82)	14.1(71)	13.2(67)
5	2.9(94)	5.0(82)	8.9(62)	11.6(57)	14.7(46)	15.9(37)
6	3.1(64)	6.4(52)	10.0(42)	11.5(42)	13.5(36)	16.3(27)
7	3.4(49)	7.7(37)	8.4(37)	12.8(27)	13.7(26)	19.2(17)
8	3.8(39)	7.2(32)	8.8(27)	11.9(22)	17.7(16)	22.0(12)
Mean(7)	3.3	6.3	8.9	12.1	15.2	17.5
	Prey mainly *Pseudocalanus minutus*					
1	3.3(203)	6.5(200)	9.1(212)	12.0(203)	13.3(217)	14.6(198)
2	3.5(173)	7.7(150)	9.4(162)	12.2(153)	14.2(147)	15.8(128)
3	3.7(153)	6.9(145)	9.8(130)	12.9(113)	15.4(107)	17.6(88)
4	2.9(143)	4.8(135)	8.3(100)	11.8(83)	12.5(87)	14.3(68)
5	2.9(103)	5.4(85)	9.6(60)	10.6(63)	14.3(52)	15.1(43)
6	3.0(83)	6.8(55)	11.6(40)	12.8(43)	16.2(37)	17.6(28)
7	3.3(63)	7.2(45)	10.5(35)	13.5(33)	14.7(32)	16.3(23)
8	3.5(53)	6.9(40)	9.9(30)	11.6(28)	14.7(25)	16.9(18)
Mean	3.2	6.5	9.7	12.1	14.4	16.0

[a]$\%\ \text{ration} = \left(\left(\frac{\text{Daily ration}}{\frac{\text{Initial wt} + \text{final wt}}{2}}\right) \times 100\right)$.

[b]Chum salmon feeding on *C. plumchrus* were on half rations for 1st week.

The electivity experiments, in which chum salmon were offered a mixture of prey sizes ranging from 0.5 to 20 mm in length, were carried out during the course of the main feeding experiment. As with other supplementary experiments, the fish were starved 24 hr before being offered a ration. The prey, including *C. pacificus*, 1.6–2.5 mm, which were omitted from the primary feeding experiments, were stirred around at the start of the experiment to ensure a homogenous distribution and then left to swim or settle depending upon their condition. In all cases there were live prey of all sizes visibly remaining in the water at the end of the feeding period. The

TABLE 2. Weekly mean wet weights (g × 100) of chum salmon fed different concentrations (percentages of wet weights of fish per day) of various prey.

	Euphausia pacifica							*Calanus plumchrus*						*Pseudocalanus minutus*							Starved	Excess	Mixed[a]
Week	3%	6	8	11	14	17	3%	6	9	12	15	17	3%	6	10	12	14	16	0	∞	≈
0	45	45	45	45	45	45	45	45	45	45	45	45	45	45	45	45	45	45	–	–	45
1	58	71	76	76	82	80	48	51	51	57	63	66	52	56	58	63	69	82	–	–	66
2	65	78	93	95	98	106	60	69	68	80	87	96	58	59	73	78	89	101	130	130	90
3	66	77	111	108	132	132	65	85	96	111	122	160	57	74	84	102	111	137	106	188	125
4	100	123	200	194	202	220	103	138	156	168	209	258	99	128	157	167	192	240	120	350	165
5	105	154	214	240	284	358	139	181	205	233	278	371	118	160	190	227	252	326	108	420	220
6	137	230	320	360	356	553	193	215	270	314	400	465	142	193	240	254	301	426	114	800	280
7	132	205	358	396	447	587	198	252	373	448	520	670	176	214	300	341	396	556	88	850	350
8	128	252	550	548	713	780	248	314	462	562	646	724	178	264	376	474	496	651	96	960	440

[a]Estimated weights for pink salmon feeding under natural conditions (data from LeBrasseur and Parker, 1964).

TABLE 3. Computed mean growth rates for juvenile chum salmon fed on various concentrations of various prey (from data in Tables 1 and 2).

Ration (% *fish wt*)	Mean weight (g)		Growth (%/*day at* $P = 0.05$)			Time (*days*)
	Initial	Final	Mean	Max	Min	
			Starved			
0	1.3	0.9	−0.7	−0.5	−0.9	42
			Excess prey, mixed sizes (0.5–20 mm)			
∞	1.3	12.7	5.4	6.2	5.0	42
			Mainly E. pacifica (6–20 mm)			
3	0.45	1.6	2.2	2.5	2.0	56
6		2.9	3.3	3.6	3.0	
8		5.8	4.6	4.8	4.4	
11		6.2	4.8	5.1	4.5	
14		7.5	5.1	5.4	4.8	
17	0.45	9.8	5.6	5.9	5.3	
			Mainly C. plumchrus (2.5–4.5 mm)			
3	0.45	2.5	3.1	3.4	2.8	
6		3.4	3.7	3.9	3.5	
9		4.8	4.3	4.5	4.1	
12		6.0	4.7	4.8	4.6	
15		7.6	5.1	5.3	4.9	
17	0.45	9.9	5.7	6.0	5.3	
			Mainly P. minutus (0.5–1.5 mm)			
3	0.45	1.9	2.6	2.8	2.4	
6		2.8	3.3	3.6	3.0	
10		4.8	4.0	4.2	3.8	
12		4.9	4.3	4.5	4.1	
14		5.8	4.6	4.8	4.4	
16	0.45	8.5	5.3	5.7	5.0	
			Variable concentrations, mixed species, and sizes[a]			
≈	0.45	5.1	4.5	4.7	4.3	56

[a]Estimates for wild pink salmon from LeBrasseur and Parker (1964).

experiments lasted 1 hr after which the fish, numbering 10–15, were killed and their stomach contents counted. The remaining zooplankton in the tanks were collected and counted, and the counts from the fish and the tank were combined to give a measure of the initial prey concentration. The purpose of the electivity experiments was to determine if the chum salmon had a preference for prey of a specific size and, if so, if the preference was modified by the fish's previous feeding experience. The electivity value, E, which may range from −1 to +1 was defined by Ivlev (1961) as the ratio of the difference between relative frequencies of a prey size category in the ration and in the tank to the sum of the two values. A zero value indicates that fish select prey in proportion to their concentration in the tank. As the value of E increases to +1, or decreases to −1, the implication is that prey are increasingly selected or avoided.

TABLE 4. Carbon and nitrogen analyses (% dry weight) of crustacean prey offered to the fish.

Date	Prey size (*mm*)					
	6–20		2.5–4.5		0.5–1.5	
	C	N	C	N	C	N
May 24	43.5	11.2	51.0	9.2	50.7	9.5
31	42.6	11.1	51.1	9.1	48.4	9.9
June 7	39.3	10.0	44.8	11.0	46.0	10.2
14	44.0	11.4	48.6	10.3	46.9	10.9
21	44.8	10.1	46.6	10.4	44.4	11.2
28	42.7	9.4	43.6	10.2	47.6	11.0
July 5	44.0	12.1	46.3	11.2	45.2	10.4
12	43.2	5.9	52.2	9.9	40.4	10.5
Mean	43.0	10.2	48.0	10.2	46.2	10.5

At no time was there any difficulty in holding the juvenile chum salmon. They readily accepted prey of each size range and, except in the tank where a surplus of zooplankton was added, there was no tank in which prey remained after 24 hr. Chum salmon, particularly the fish less than 60 mm, had some difficulty feeding upon euphausiids. It usually took a fish several attacks to get the euphausiid in a line parallel to the fish where it could be swallowed and when the euphausiid was swallowed frequently a portion would remain for a period of time projecting from the fish's mouth.

The mortality was low for all fish offered prey, approximately 2% for each group over the 8-week feeding period. The mortality was attributed to handling when the tanks were cleaned and, later, when the fish were larger, to fish jumping out of the tanks. The latter was prevented by placing clear plastic over the open end of the tanks. The starved fish had a higher total mortality, 16%, all of which took place during the last 3 weeks, June 22–July 12.

Some prey organisms were carried out of the tanks with the overflow. This loss was found to amount to less than 1% of the prey put into the tanks. Since the amount of the prey lost represents only a small fraction of the ration, no attempt was made to adjust for it.

Though no zooplankton were offered to the starved chum salmon, stomach contents from samples of these fish were examined weekly. Occasionally, some stomachs would contain small organisms, a maximum of 100 organisms less than 0.5 mm long, but most stomachs were empty. Monitoring the inflow indicated that an estimated 40–70 microzooplankton were carried into the tanks every hour. No doubt this estimate is subject to wide variation but as is shown below insufficient material was carried into the tank to maintain the initial weight of the starved fish.

The salmon readily took the prey offered whether it was alive or dead, drifting in the current or resting on the bottom. It is assumed that the chum salmon consumed all the prey which were offered, except in the case of excess feeding, and that these prey were their only source of food.

RESULTS

There is an obvious association between the growth rate and prey concentration for fish held on different rations (Table 3, Fig. 1). The starved chum salmon lost weight over a 6-week period at 0.7% per day whereas fish on excess rations increased in weight at 5.4% per day. The growth rates for chums held on fixed rations ranged from 2.2 to 5.7% per day with the ration increasing from 3 to 17%. The size of prey did not significantly affect the

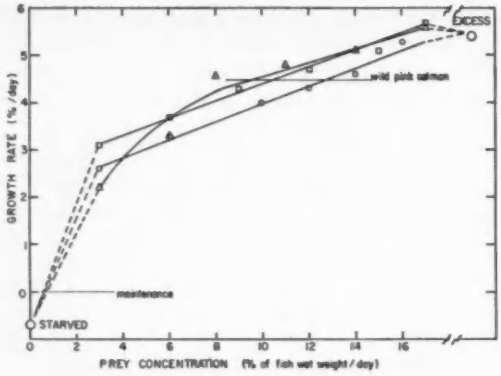

FIG. 1. Growth rates (% increases in weight per day) for chum salmon held 8 weeks on fixed rations of *E. pacifica* (△), *C. plumchrus* (□), and *P. minutus* (○) (data taken from Table 3). The lines were fitted by eye. Data for wild pink salmon were taken from LeBrasseur and Parker (1964).

growth rate for the 8-week period. Chum salmon feeding on the lowest concentration of euphausiids experienced the lowest rate of increase in weight, but on increasing euphausiid concentrations the rate equalled or exceeded that of chums held on other prey. The best apparent prey for the growth of chum salmon was *C. plumchrus*, whereas the poorest overall rate of growth was for fish held on *P. minutus* prey. However, these computed growth rates as reported in Table 3 were not statistically different at $P = 0.05$. It is of interest to note that the maintenance ration as implied by extrapolation between the points for starved fish and fish on the 3% ration lies between 0.4 and 1% (Fig. 1), the higher limit being for juvenile chums feeding on euphausiids. The comparable growth rate for wild pink salmon was estimated to be 4.5% per day, which would require an estimated ration of 10–12% of their weight per day.

No statistically significant differences in the final dry weight of the fish held on the different prey were found. Consequently, the data for fish offered different prey were combined and the effect of ration size, or prey concentration, was examined. At the start of the experiment the per cent dry weight values for all fish in the 20 tanks was 15.8 ± 2%. The per cent dry weight remained relatively constant for the first 5 weeks. By the 6th week there was a clear difference between the dry weight of fish on the lower rations (tanks 1–3) and that of fish on the higher rations (tanks 4–6). This difference was maintained through to the end of the experiment, at which time the chum salmon in tanks 4–6 had a dry weight equivalent to 20.6% of the wet weight whereas the per cent dry weight of fish in tanks 1–3 had not significantly changed from the initial determinations, i.e., there was an approximately 30% increase in dry weight for fish in tanks 4–6. The dry weight for starved chum salmon decreased to 12.2% of the wet weight by the end of the experiment whereas that for fish offered an excess ration increased to 22.2%. Observations made on wild chum salmon collected in June and July indicated a relatively constant dry weight of 19.0%.

For the purpose of this report, it is unnecessary to correct for the change in percentage dry weight; it is sufficient to note that the quantity of rations consumed can bring about substantial changes in the dry weight composition of chum salmon.

Chum salmon stomach contents were examined weekly except for the weeks of June 21 and 28, for those fish being reared on the three prey size fractions and the fish which were offered no rations. The ratio of weight of stomach contents to fish weight was lowest for fish feeding on *P. minutus*. The quantity of prey ingested was not related (or only slightly so) to the concentration of prey in the tanks (Fig. 2). For chums being offered euphausiid

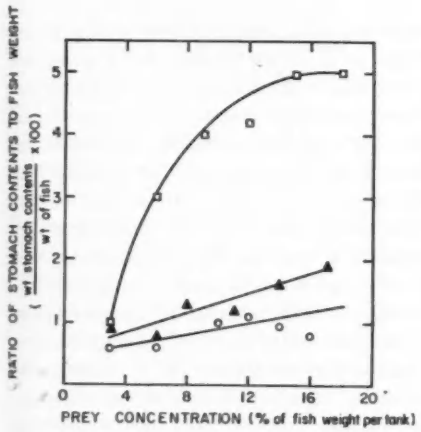

FIG. 2. Relations between the ratio of weight of stomach contents to fish weight after 2 hr feeding and the concentrations of three kinds of prey in the tanks (*E. pacifica* ▲, *C. plumchrus* □, *P. minutus* ○). The lines were fitted by eye.

rations the level of the biomass in the stomachs increased slightly with increasing prey concentration up to approximately 2% of the fish weight. In contrast, where *C. plumchrus* was offered as prey the weight of stomach contents increased rapidly for fish in tanks 1–4 and levelled off at approximately 5% of the fish weight at subsequent prey concentrations in tanks 5 and 6. The maximum weight of prey in a chum salmon stomach was found to be 6.3% of the body weight and therefore the weight of stomach contents might be expected to level off between 5 and 6% of the body weight. These results, although based upon the mean of five sampling periods, are reproducible for any particular sampling date after the first, when the *C. plumchrus* rations were too low. It is apparent that chums feeding upon *C. plumchrus* can readily obtain a greater weight of prey within 2 hr than those fish feeding upon *P. minutus* or *E. pacifica* provided each prey is digested at the same rate.

A preliminary experiment was carried out to determine relative digestion rates. The results indicate that *P. minutus* is passed from the stomach into the intestines more rapidly than *C. plumchrus* or *E. pacifica*. This finding, although qualitative, indicates that the actual consumption of *Pseudocalanus*

in chum salmon stomachs is probably greater relative to rates of feeding on the other foods than is indicated by the simple comparison of weights in the stomach after 2 hr.

Neither the fish nor the prey exhibited any noticeably different behaviour in the electivity experiments as compared with the more usual tank situation described earlier. The selection of prey was apparently a matter of choice by the fish. It should be noted, however, that *Calanus* sp. was in most experiments (Ce, Dd, De excepted) the most abundant and, presumably, the most available prey by weight in the tanks and that it was the predominant prey in the stomachs (Table 5). There was not, however, a correlation between amount of each kind of prey in the tanks and the corresponding amounts of prey in the fish stomachs.

Prey less than 1.5 mm (*P. minutus*) elicited a negative response in every experiment where a choice was available, and in spite of a fish's previous feeding history, chum salmon selected prey larger than 1.5 mm. Prey ranging from 1.6 to 4.5 mm (*Calanus* sp.) elicited a positive response from nearly all groups of chum tested. Of special interest were the fish tested at the beginning and end of the feeding trials. These fish had, at the most, very limited feeding experience but when offered a mixed ration of prey sizes they selected the *Calanus* size fraction. Euphausiids were positively selected only by fish which had previously been feeding upon a euphausiid ration. The exception to this was in electivity experiments in which only two sizes of prey were available, *P. minutus* and *E. pacifica*, and in this instance fish which had usually eaten *Calanus* sp. switched to euphausiids. Inspection of the electivity values for large prey (12–20 mm) suggests that as the chums increased in length, the large prey formed an increasing proportion of the stomach contents. Experiments, not shown here, with wild chum salmon, again indicated a positive selection of the *Calanus* sp. prey fraction. A most significant feature of the electivity experiments is the absence of a strong positive preference, as indicated by a value of E greater than 0.5, for any of the prey except in trials Ce and De, the proportions of *positively* selected prey in fish and tank being approximately the same.

DISCUSSION

The steady decline in the growth efficiency with increasing rations which is evident from Fig. 1 confirms the K-line of Paloheimo and Dickie (1966). Furthermore, it is apparent that no significant effect between the type or size of prey and the rate of growth could be substantiated under the present experimental conditions. There is a suggestion from the extrapolated portion of the curves for rations near the maintenance ration that the effect of prey size might be strongest where prey are in reduced concentrations. This raises a fundamental objection to the type of experiment reported here. The fish and the prey were together in a confined space. At the lowest ration, 3.3 g/250 liters, the equivalent numbers of prey were 160 *P. minutus*, 13 *C. plumchrus*, and 0.6 *E. pacifica* respectively per liter, i.e., high concentrations which

are infrequently encountered in nature. Increasing the prey concentrations represents increasingly unnatural predator–prey situations. This experimental design undoubtedly reduced the effort required for capturing prey and thereby may have masked any relationship between prey size and growth. In addition. the relationship between growth and ration must underestimate the actual relation for wild fish feeding on natural zooplankton populations, since the experimental situation represents prey concentrations higher than those normally reported. However, if consideration is given to Ivlev's theory (Ivlev, 1961) that an increase in the patchiness of prey assists fish in obtaining a larger ration, then the feeding experiments reported here might be considered to have simulated a very high prey contagion factor, rather than a high prey density in toto. If this is true, then under natural conditions the results in Fig. 1 show that prey of different size can support the same growth rate of fish when the energy required to collect the prey is small, due to the prey being highly concentrated, such as might occur in a plankton patch. The occurrence (in situ) of plankton patches has been clearly demonstrated by Cassie (1959, 1963) and Colebrook (1960).

Figure 2 confirms previous studies (Parsons and LeBrasseur, 1968), showing that the stomach contents reflect in part the type and concentration of prey, the very small and the very large prey being apparently less readily captured than *C. plumchrus* as shown by the examination of stomachs after a short time interval, i.e., 2 hr. For chum salmon to maintain the same rate of growth on other prey as on *C. plumchrus* would require either feeding over a longer period or prey which is nutritionally superior. In Table 4 it is shown that all prey were nutritionally similar. Consequently, the rations taken by the fish feeding on *P. minutus* and *E. pacifica* must be taken over a longer period of time. This in turn implies that under natural feeding conditions it becomes even more difficult for young chum salmon to find adequate rations when *C. plumchrus* or an equivalent prey are absent or scarce.

The results of the electivity studies reinforce the inferred association between chum salmon and *C. plumchrus*. As reported above, the previous feeding history of the juvenile salmon influenced the choice of prey to the extent that fish "trained" on euphausiids selected euphausiids. However, all fish, with and without feeding experience, tended to avoid the small prey and selected *Calanus* sp. and, to a lesser extent, euphausiids. In the case of selecting euphausiids, it is noteworthy (Table 5, De) that only in the instance where there was a choice of two sizes of prey (but no *Calanus* sp.) was there a positive electivity value for euphausiids exceeding 0.5. In all other cases, electivity tended to be only slightly positive, indicating that when chum salmon are given prey of suitable size (i.e., *Calanus*), they select the prey in proportion to its abundance.

The early sea life of juvenile salmon usually coincides with the period of maximum *C. plumchrus* biomass in the coastal waters of British Columbia. It is therefore interesting to speculate on the effects of changes in the availability of *C. plumchrus* on the feeding behaviour of the fish. The kind and quantity

TABLE 5. Electivity values for juvenile chum salmon of various lengths offered a mixture of prey after being fed on a particular prey. T and S are, respectively, the percentages of the total weights of prey placed in the tanks and of the total weights of prey found in the stomachs of 10–15 fish after feeding in the tank for 1 hr.

Size ranges[a] of prey (*mm*) offered	S	T	E[b]	S	T	E	S	T	E	S	T	E	S	T	E
							A. Fish that were not offered food								
				(*a*) 41 mm (Initial feeding)			(*b*) 46 mm (Starved for 6 weeks)								
0.5–1.5				5	5	0	3	35	−.84						
1.6–4.5				91	65	.17	96	53	.29						
6–12				2	8	.60	1	2	−.33						
12–20				2	22	−.80	0	10	−1.0						
							B. Fish that had fed on prey 0.5–1.5 mm, mainly P. minutus								
	(*a*) 56 mm			(*b*) 58 mm			(*c*) 65 mm			(*d*) 69 mm					
0.5–1.5	14	17	−.10	23	27	−.08	15	36	−.41	9	36	−.60			
1.6–4.5	86	61	.17	60	47	.12	62	39	.23	68	42	.24			
6–12	Trace	Trace	0	15	13	.07	22	13	.26	12	6	.33			
12–20	0	22	−1.0	2	12	−.73	1	9	−.80	11	16	−.18			

C. Fish that had fed on prey 2.5–4.5 mm, mainly C. plumchrus

	(*a*) 54 mm			(*b*) 61 mm			(*c*) 69 mm			(*d*) 73 mm			(*e*) 80 mm		
0.5–1.5	4	11	−.47	7	23	−.53	15	37	−.42	6	15	−.37	18	80	−.63
1.6–4.5	81	62	.13	69	44	.22	68	46	.19	70	54	.13	0	0	
6–12	Trace	Trace	0	12	9	.14	13	9	.18	11	9	.10	0	0	
12–20	15	27	−.28	12	24	−.33	4	8	−.33	13	22	−.26	82	20	.57

D. Fish that had fed on prey 6–20 mm, mainly E. pacifica

	(*a*) 55 mm			(*b*) 56 mm			(*c*) 63 mm			(*d*) 79 mm			(*e*) 57 mm		
0.5–1.5	4	10	−.43	4	20	−.67	2	25	−.85	2	18	−.80	32	80	−.43
1.6–4.5	30	45	−.20	47	42	.06	67	52	.13	32	29	.05	0	0	
6–12	1	2	−.33	10	6	.25	Trace	Trace	0	33	20	.24	0	0	
12–20	65	42	.12	39	32	.10	31	23	.15	33	33	0	68	20	.54

[a]For a constant wet weight of 25 mg the equivalent numbers of organisms were:

Length (*mm*)	0.5–1.5	1.6–4.5	6–12	12–20
No.	300	25	4	1

[b]$E = \frac{S - T}{S + T}$ = electivity index.

of phytoplankton available as food for herbivorous crustaceans, such as *C. plumchrus*, *P. minutus*, and *E. pacifica* has been demonstrated to limit the growth of some herbivorous species while favouring the growth of other species (Parsons et al., 1967). Thus a decrease in availability of *C. plumchrus* may result from the presence of a phytoplankton species that favours the production of smaller or larger herbivores. Feeding upon small prey such as *P. minutus* would require a high degree of prey contagion and nearly continuous feeding. Feeding upon euphausiids would be mainly restricted to darkness, since this is generally the only period when euphausiids are available near the surface. There is, of course, a great variety of other zooplankton species which serve as food and which would modify the effects of variations in the availability of particular prey species. However, it seems reasonable to postulate that the degree to which young fish may be shifted away from an optimum prey will be reflected in the growth of the fish, and further that poor growth would allow greater predation upon the fish.

It is apparent from the experiments reported here that further feeding trials are required. It is planned to rear juvenile salmon in large tanks in which prey equivalent to 1% of the fish weight, i.e., just over the maintenance ration, are present at differing degrees of contagion and in which the fish will be forced to spend energy searching for their prey.

ACKNOWLEDGMENTS

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Sustained Swimming Ability of Larvae of Walleye (*Stizostedion vitreum vitreum*) and Yellow Perch (*Perca flavescens*)

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HOUDE, EDWARD D. 1969. Sustained swimming ability of larvae of walleye (*Stizostedion vitreum vitreum*) and yellow perch (*Perca flavescens*). J. Fish. Res. Bd. Canada 26: 1647–1659.

Sustained swimming ability of limnetic larvae of walleye and yellow perch from Oneida Lake, New York, was compared in an experimental apparatus. The current velocity that 50% of the larvae could sustain in 1-hr tests was recorded for each 1-mm length class. Yellow perch larvae swam better than walleye larvae for length classes less than 9–10 mm total length (TL), but swimming ability of the two species was equal for length classes from 9 to 15 mm. Velocities that larvae under 9.5 mm TL could sustain were less than 3.0 cm/sec, and it was concluded that newly hatched young of both species would be subject to transport by lake currents of greater velocity. Relative swimming ability, expressed as the number of body lengths/sec that a larva could sustain for 1 hr, approached an asymptote between 3 and 4 lengths/sec for larvae longer than 9.5 mm. The greater swimming ability of newly hatched yellow perch larvae, compared with that of walleyes, appeared to be related to the smaller yolk sac of yellow perch at hatching.

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INTRODUCTION

LARVAE OF WALLEYE AND YELLOW PERCH in Oneida Lake, New York, hatch in early May. Both species are limnetic for approximately 5 weeks, both behave photopositively during this time, but their spatial distributions are different. Yellow perch larvae are widely distributed in the lake (Noble, MS, 1968), but walleye larvae become concentrated in bays along the south shore about 10 days after hatchery release. Swimming ability of the larvae was considered in examining distributional differences, and success of walleye in maintaining themselves within the bays was thought to be related to better swimming ability than that of yellow perch. In this study an experimental comparison has been made of the sustained swimming abilities of walleye and yellow perch larvae from the time of hatching until they were approximately 1 month of age and no longer limnetic.

Swimming ability of larval fishes, excluding salmonids, has rarely been studied because of the difficulty of rearing and handling the delicate and easily injured larvae. Toetz (1966) observed swimming behavior and measured

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movements of bluegill larvae (*Lepomis macrochirus*) in aquaria. The effect of acclimation temperature on swimming of young smallmouth bass (*Micropterus dolomieui*) was recently examined (Larimore and Duever, 1968), but the fish were relatively large (20–25 mm total length (TL)). Bishai (1960) reported on the sustained swimming ability of pelagic newly hatched marine herring larvae (*Clupea harengus*), and concluded that 6.5–8-mm larvae could sustain currents of 0.58 cm/sec but drifted with swifter currents. Blaxter (1962) and Blaxter and Dickson (1959) also made estimates of maximum swimming speeds of herring larvae. Ryland (1963) concluded that newly hatched plaice larvae (*Pleuronectes platessa*) of about 7.0 mm could swim against 1.5 cm/sec currents, with an increase in ability to 9.0 cm/sec for older larvae about 13 mm long.

Development of larval walleyes and yellow perch was described by Norden (1961). Walleye larvae hatch at about 7.5 mm in Oneida Lake, but yellow perch larvae hatch at about 6.0 mm. A relatively greater amount of yolk is present in walleye prolarvae than in yellow perch. In other respects the two species are similar in appearance at hatching, although the number of postanal myomeres of walleyes exceeds that of yellow perch larvae (Norden, 1961). Yolk reserves are exhausted in yellow perch at approximately 7.0 mm, but some yolk may be present in walleyes to lengths of 9.5 mm.

METHODS

The usual types of apparatus employed to test swimming ability and stamina of fish (e.g., Bainbridge, 1958; Brett, 1964; Fry, 1957; MacLeod, 1967) are not easily adaptable for use with small and delicate larvae. Bishai (1960) designed an apparatus to test the effect of water currents on the larvae of two marine species, and his device has been slightly modified to suit the needs of the present experiment (Fig. 1). The apparatus consists of a series of 19-mm diam glass tubes and four 13-mm nalgene needle valves to regulate flow. Larvae were introduced into the experimental tube through the funnel and were maneuvered into the 50-cm clear area where they were tested. Both ends of the experimental tube were blocked with #00 mesh nylon screen to prevent larvae from being washed out of the tube and to reduce turbulence of flow in the tube.

Water was supplied to the experimental device by a closed, recirculating system (Fig. 2). Temperature was controlled and maintained at 13 ± 0.5 C, which was within 2 C of the mean lake temperature during May and early June in 1965–67. The system was filled to capacity with 570 liters of lake water, which was filtered through #10 plankton netting to remove large particles, and 57 liters was replaced with fresh water every day.

Water flowed by gravity feed from the header tank into the experimental apparatus. By adjustment of valves, currents could be made to flow in either direction in the tube at velocities of from near zero to more than 100 cm/sec. Valves 3 and 4 (Fig. 1) were calibrated by measuring the volume of water delivered in a timed period at marked valve positions. The amount delivered per unit time divided by the cross-sectional area of the tube gave the average velocity of flow through the tube for each valve position. Mean velocities from five trials at each valve position were calculated. A linear regression of log velocity on log valve position was fitted by least squares to allow determination of velocity for any position of the valve. Small quantities of dye placed in the tube confirmed the reliability of the regressions as predictors of velocity.

Walleye and yellow perch larvae were hatched from eggs incubated in petri dishes and were transferred to 76-liter aquaria or 3-m diam plastic pools for use in the swimming experiments. Additional larvae of both species were collected at night in the lake after being attracted to artificial light (Schumann, 1963). Larvae fed actively on mixed zooplankton collected from the lake in a #10 mesh 0.5-m net.

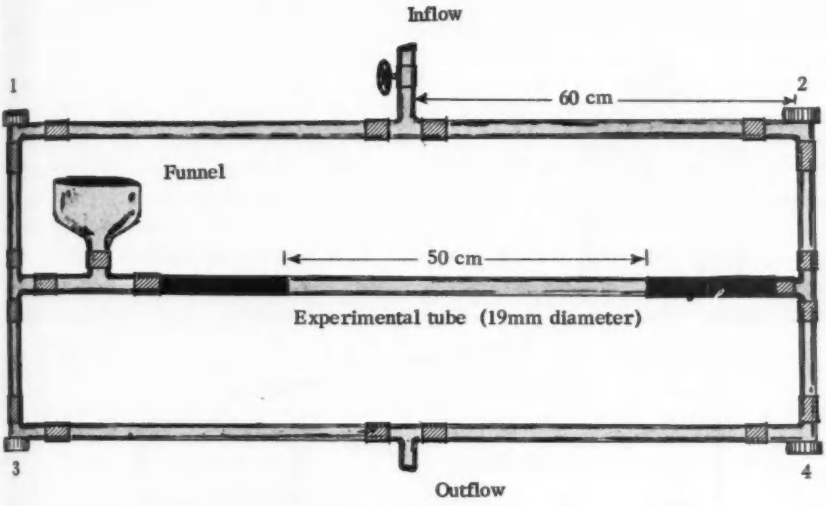

FIG. 1. Experimental apparatus used to test swimming ability of larvae.

1967 TEST METHODS

Larvae were transferred to an aquarium which was held at 13 ± 2 C at least 4 hr before being introduced into the experimental tube at 13 C. They were allowed to acclimate in the tube for 10 min with water slowly trickling through at insignificant velocity, before the current was adjusted to the test velocity. Velocities used in the study were 1.0, 2.5, 5.0, and 7.5 cm/sec. In 1967, larvae were placed in the tube singly and tested at a given velocity for up to 1 hr. If they washed out of the 50-cm test length before an hour had passed, the failure time was recorded. If they swam for an hour the test was terminated and the larvae were considered successful.

Either 5 or 10 larvae in each 1-mm length class were tested at each current velocity, unless it was obvious that 100% success or failure would occur at a particular velocity. For example, if all 10 larvae in a length class failed to swim for 1 hr at 5.0 cm/sec, no larvae in this class were tested at 7.5 cm/sec; or if all of the larvae in a length class successfully sustained currents of 2.5 cm/sec, there was little need to test larvae at 1.0 cm/sec. Only a few larvae longer than 15 mm were available. A total of 181 walleyes from 7.0 to 22.2 mm and 137 yellow perch from 6.0 to 18.1 mm were tested in 1967.

Determination of sustained swimming ability can be viewed as a bioassay experiment (Brett, 1967). Current velocities are analogous to dose rates, and the velocity at which 50% of the larvae of a length class failed (FV_{50}) is comparable to an LD_{50}. For length classes where sufficient data were available, the method of Litchfield and Wilcoxon (1949) was applied to estimate the 1-hr FV_{50} and the confidence limits on the estimate. The FV_{50} values at each length class were determined for both walleye and yellow perch larvae in 1967, but data from 1966 preliminary experiments were not suitable for the bioassay analyses.

1966 PRELIMINARY TEST METHODS

In the 1966 preliminary work, the test period length was 10 min except for a few tests of 3-hr duration. Walleye larvae were exposed to current velocities and whether they drifted, swam against, or held position in the current was noted. If they drifted, the average rate of drift was recorded by timing the drift over a measured distance of the tube for three trials. If a larva held position against the current, the experiment was terminated after 10 min. In the period May

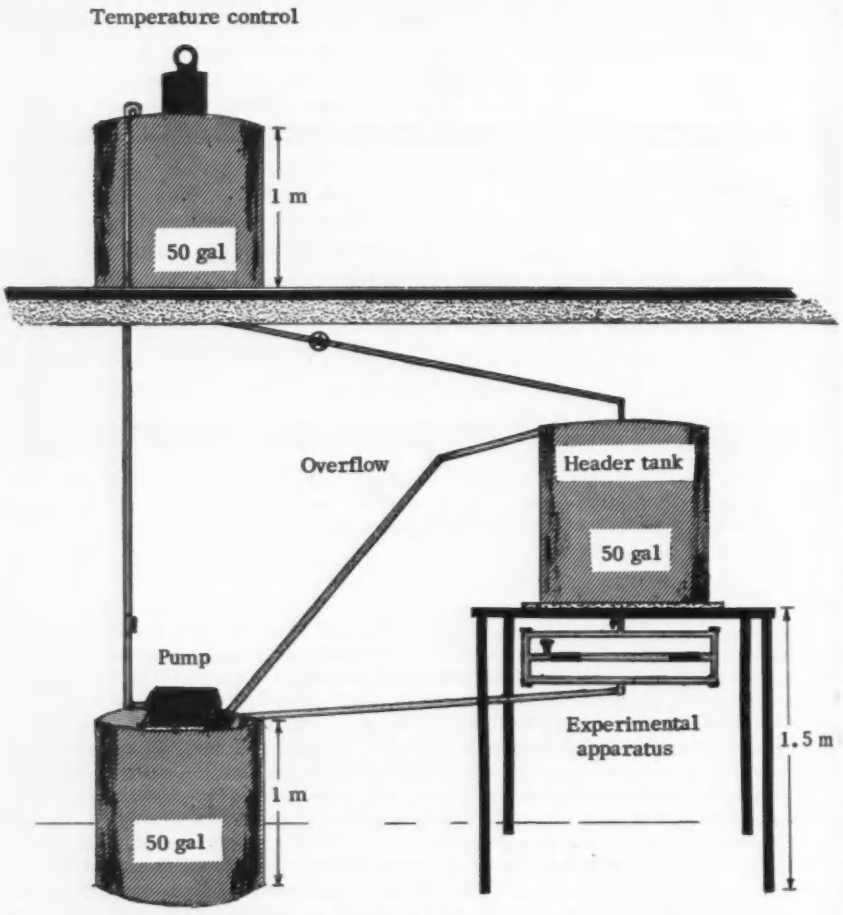

FIG. 2. Experimental system, including testing apparatus, water supply, and temperature control.

1–June 5, 1966, 164 larvae, 7.0–13.0 mm, were tested by this technique. Twenty-one larvae, 12.1–22.5 mm, were used in 3-hr sustained swimming tests at 5.0 and 7.0 cm/sec current velocities. Temperatures were not controlled in 1966 and ranged from 12.8 to 20 C.

RESULTS

1966 OBSERVATIONS

Preliminary tests were conducted in 1966 to determine the behavior and response of walleye larvae exposed to currents. When a current flowed through the tube most larvae immediately faced into it. Lights in the lab provided visual clues, and the occasional touching of their dorsum to the

top wall of the tube provided a tactile clue. The average velocity in a tube of 9.5 mm radius occurs at 8.22 mm from the center. Because larvae usually swam in the top half of the tube and their maximum body depths ranged from 1.5 mm at 8.0 mm TL to 2.8 mm at 14.5 mm TL, they swam in the region of the tube where velocities were near the mean value. The vertical gradient of velocities that exists over the cross section of a tube from the walls to the center, and which is steepest near the walls, provided an additional clue for orientation by larvae.

Most walleye larvae less than 12.0 mm drifted with the current in the tube when velocities exceeded 0.5 cm/sec (Table 1). Larvae demonstrated

TABLE 1. Swimming ability and behavior of various sizes of walleye larvae in experimental current apparatus, 1966, in 10-min tests.

Length class (*mm*)	No. of larvae tested	Current velocity (*cm/sec*)	% swimming against	% holding position	% drifting	Avg drift speed (*cm/sec*)	Larval drift rate/ current velocity
7.0–7.9	5	0.5	No response or random swimming in tube				
	4	1.0	0	0	100	0.86	0.86
	18	2.0	5.6	5.6	88.8	1.22	0.61
	5	3.0	0	20.0	80.0	2.30	0.77
	12	5.0	0	0	100	3.84	0.77
	5	7.0	0	0	100	7.98	1.14
8.0–8.9	1	0.5	0	100	0		
	31	2.0	25.8	3.2	71.0	1.82	0.91
	3	3.0	33.3	0	66.7	1.38	0.46
	22	5.0	0	0	100	4.10	0.82
9.0–9.9	1	2.0	100	0	0		
	19	3.0	36.8	5.3	57.9	1.16	0.39
	22	5.0	0	0	100	3.94	0.79
10.0–10.9	3	3.0	33.3	0	66.7	0.38	0.13
	3	5.0	0	0	100	4.45	0.89
11.0–11.9	1	3.0	0	100	0		
	1	5.0	0	0	100	0.36	0.07
12.0–13.0	4	3.0	75	0	25	0.30	0.10
	4	5.0	75	0	25	3.87	0.77

rheotaxis by facing into the current and swimming but usually were carried backwards by the current. An increasing percentage of larvae stemmed or swam against currents as size of larvae increased. Drift of newly hatched larvae of 7.0–7.9 mm at velocities of 7.0 cm/sec was uncontrolled, and this was reflected in the drift rate which exceeded the test velocity (Table 1).

Uncontrolled drift was characterized by the failure of a larva to orient and consequently, by a tumbling drift near the center of the tube, where the current velocity was twice the mean velocity.

Although most larvae drifted in currents of 2.0–7.0 cm/sec, they began to swim vigorously when approaching the end of the experimental tube. This response also occurred after the ends of the tube were covered with black tape. Walleye larvae were maneuvered into the clear area between the taped portions where they swam until fatigued rather than allowing themselves to be carried into the dark taped area.

Sustained swimming tests were carried out by introducing a larva into the tube and allowing it to swim against a current velocity until it fatigued or for 3 hr. Of 21 larvae, 12.1–22.5 mm, tested at temperatures from 16.7 to 20 C and current velocities of 5.0 and 7.0 cm/sec, four larvae, 13.2–14.0 mm, swam at 5.0 cm/sec for 3 hr. Two larvae, 16.7 and 17.9 mm, tested at 7.0 cm/sec, successfully sustained the current for the 3-hr period.

1967 Results

Tests in 1967 were designed to determine sustained swimming ability of both walleye and yellow perch larvae. A few yellow perch larvae had been observed in the apparatus in 1966, and their behavior was similar to that of walleyes but more erratic. Most perch larvae under 6.5 mm appeared to be swimming actively in the aquarium, but their swimming movements ceased after they were introduced into the apparatus. These larvae did not respond to currents but allowed themselves to be rolled along the length of the tube by the current. Walleye larvae, at all sizes tested, responded well to currents in the tube.

The distribution of responses (swimming times) at each of the four test current velocities was plotted against length of larvae for both species. The most striking result was the great variation in swimming times of larvae of equal lengths at a given current velocity. This variation is illustrated by the responses of walleye and yellow perch larvae tested at 5.0 cm/sec (Fig. 3 and 4). Responses for larvae of a given length were more variable at 5.0 and 7.5 cm/sec than at 1.0 and 2.5 cm/sec.

The great variation in responses made regression analysis a poor choice for comparing swimming ability of the two species, but analyses similar to those used for data from bioassay experiments proved to be useful. Percentages of larvae failing to swim in the tube for the 1-hr test period were plotted against current velocity for each length class. Typical sigmoid curves resulted, which were replotted on log-probability paper and treated by the method of Litchfield and Wilcoxon (1949) to estimate the 1-hr FV_{50} (velocity at which 50% failed) and confidence limits on the estimate for each length class where the data were suitable (Table 2). FV_{50} increased with length for both species (Fig. 5). Sustained swimming ability of yellow perch was greater than that of walleye larvae for the shortest length classes, but at 9–10 mm the two species had equal ability. The increase in sustained swimming ability of yellow perch larvae

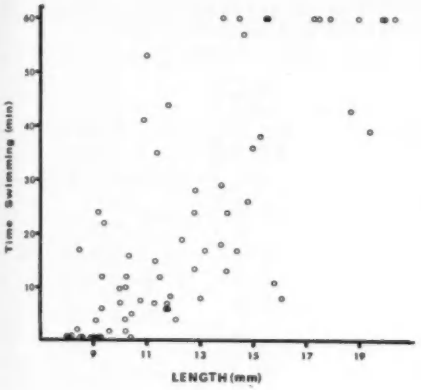

FIG. 3. Individual swimming response times of walleye larvae to current of 5.0 cm/sec in 1-hr tests.

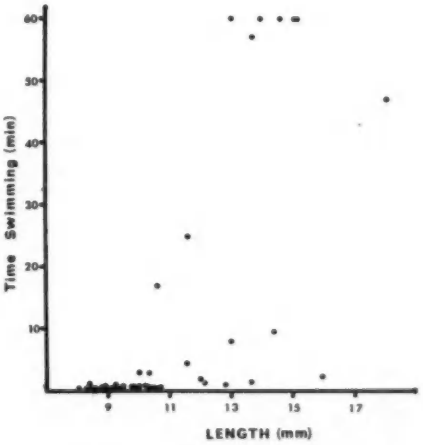

FIG. 4. Individual swimming response times of yellow perch larvae to current of 5.0 cm/sec in 1-hr tests.

was nearly linear over the length classes from hatching until 14 mm. Swimming ability of walleye larvae increased exponentially between 7.0 and 9.5 mm, but further increase in ability was linear. Few yellow perch larvae longer than 14 mm were tested. However, enough walleyes over 16 mm TL were tested at 5.0 and 7.5 cm/sec to allow the conclusion that larval walleyes of 20 mm could sustain currents of at least 7.5 cm/sec at 13 C.

Literature on sustained swimming speeds of many juvenile and adult fishes, summarized by Bainbridge (1960), indicated that swimming speed usually ranges from 3 to 6 body lengths/sec. Bainbridge also demonstrated on three species that, for long swimming times, the relative sustained speed in number of body lengths/sec becomes asymptotic at 3–4 lengths/sec. The ratio of FV_{50} (cm/sec) to length (cm) for larval walleyes and yellow perch estimates the current velocity in body lengths/sec which larvae could sustain

TABLE 2. Calculated current velocities at which 50% of walleye and yellow perch larvae failed (1-hr FV_{50}) and confidence limits on the estimate of 1-mm length classes.

Length (mm)	Walleye 1-hr FV_{50} (cm/sec)	95% confidence limits	Yellow perch 1-hr FV_{50} (cm/sec)	95% confidence limits
6.00–6.99	–	–	−0.55	–
7.00–7.99	−0.50	–	1.40	$1.00 \leq FV_{50} \leq 1.96$
8.00–8.99	1.30	$1.10 \leq FV_{50} \leq 1.54$	2.40	$2.02 \leq FV_{50} \leq 2.86$
9.00–9.99	2.90	$1.69 \leq FV_{50} \leq 4.96$	2.75	$2.41 \leq FV_{50} \leq 3.14$
10.00–10.99	3.20	$2.58 \leq FV_{50} \leq 3.97$	−3.20	–
11.00–11.99	−3.75	–	–	–
12.00–12.99	–	–	–	–
13.00–13.99	4.20	$3.47 \leq FV_{50} \leq 5.08$	4.60	$3.96 \leq FV_{50} \leq 5.34$
14.00–14.99	4.60	$4.04 \leq FV_{50} \leq 5.25$	–	–
15.00–15.99	5.00	$4.20 \leq FV_{50} \leq 5.95$	–	–

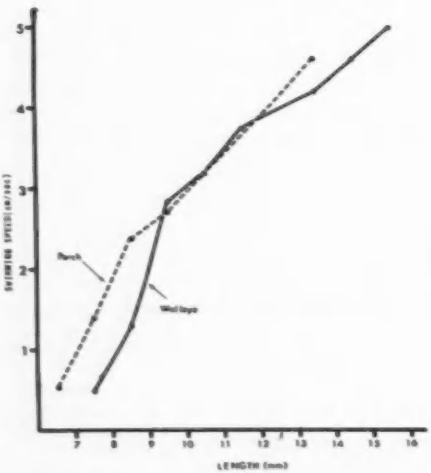

FIG. 5. Relation of swimming speed in cm/sec to fish length for walleye and yellow perch larvae. (Swimming speed is the calculated current velocity that is sustained for 1 hr by 50% of the fish (1-hr FV_{50}).)

for 1 hr. Swimming ability has been expressed in this manner (Table 3 and Fig. 6) for each length class in which suitable data were available. Both species swam poorly as newly hatched larvae, but as growth was accompanied by absorption of yolk, development of the fins, and an increased proportion of muscle, sustained ability approached the asymptotic value predicted by Bainbridge (1960) of 3–4 lengths/sec. The greater swimming ability of yellow perch compared to walleye larvae for lengths over 6.5 mm but less than 9.5 mm (Table 2 and Fig. 5) was reflected in the analysis.

TABLE 3. Swimming speeds (in body lengths/sec) sustained for 1 hr by walleye and yellow perch larvae for various sizes of fish. Values are calculated from data in Table 2.

Body length (*cm*)	Walleye		Yellow perch	
	FV_{50}: length (*body lengths/sec*)	95% confidence limits	FV_{50}: length (*body lengths/sec*)	95% confidence limits
.65	–	–	.55/.65 = 0.85	–
.75	.50/.75 = 0.67	–	1.40/.75 = 1.87	$1.33 \leq \frac{FV_{50}}{L} \leq 2.61$
.85	1.30/.85 = 1.53	$1.29 \leq \frac{FV_{50}}{L} \leq 1.81$	2.40/.85 = 2.80	$2.38 \leq \frac{FV_{50}}{L} \leq 3.36$
.95	2.90/.95 = 3.05	$1.78 \leq \frac{FV_{50}}{L} \leq 5.22$	2.75/.95 = 2.90	$2.54 \leq \frac{FV_{50}}{L} \leq 3.31$
1.05	3.20/1.05 = 3.05	$2.46 \leq \frac{FV_{50}}{L} \leq 3.78$	3.20/1.05 = 3.05	–
1.15	3.75/1/15 = 3.26	–	–	–
1.25	–	–	–	–
1.35	4.20/1.35 = 3.11	$2.57 \leq \frac{FV_{50}}{L} \leq 3.76$	4.60/1.35 = 3.41	$2.93 \leq \frac{FV_{50}}{L} \leq 3.96$
1.45	4.60/1.45 = 3.17	$2.79 \leq \frac{FV_{50}}{L} \leq 3.62$	–	–
1.55	5.00/1.55 = 3.23	$2.71 \leq \frac{FV_{50}}{L} \leq 3.84$	–	–

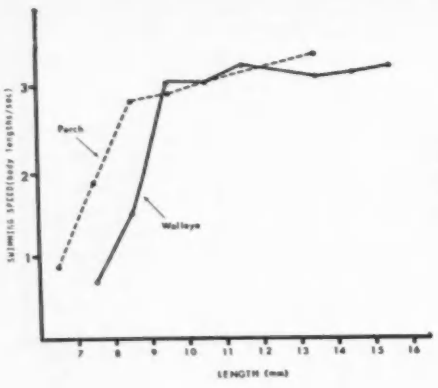

FIG. 6. Relation of swimming speed in body lengths/sec to fish length for walleye and yellow perch larvae. (Swimming speed is the calculated velocity that is sustained for 1 hr by 50% of the fish.)

DISCUSSION

The usefulness of the bioassay technique to determine sustained swimming ability of developing larval walleyes and yellow perch lies in its ability to adequately treat the variation of response which was common among larvae tested in a given length class. In experiments of this type some larvae cannot be stimulated to respond well to currents in the apparatus, but such individuals cannot be eliminated from any analysis without throwing suspicion on the final conclusions. It may be that similar variation of individuals in response to currents exists in the lake environment.

Effects of temperature on sustained swimming have been well documented (Brett, 1967; Brett et al., 1958; Fry and Hart, 1948). Optimum temperatures exist for best swimming performances by each species that has been tested. The 13 C temperature at which tests were run on walleye and yellow perch larvae averaged 2 degrees C below the mean lake temperature for the month after hatching of walleye larvae. Temperatures in the experimental apparatus were believed to represent the lake situation for larvae up to 12 mm. A quick rise in lake temperatures typically occurs during early June. Swimming performances of walleye larvae longer than 12 mm indicated that they apparently swam better at the higher temperatures of 16.7–20 C in the 1966 3-hr sustained swimming tests, than they did in 1967 at 13 C. Larvae of 12–13 mm sustained currents of at least 5.0 cm/sec in 1966, compared with an ability of only 4.0 cm/sec for larvae of the same size in 1967.

Hergenrader and Hasler (1967) noted a linear increase in swimming speed of adult yellow perch in Lake Mendota in response to temperature increases, with a Q_{10} of 1.5. Swimming ability of walleye and yellow perch larvae was calculated for 18.3 C, the mean of the 1966 experimental temperature range, using the 1967 observations of swimming ability at 13 C and assuming a Q_{10} of 1.5. Calculated swimming velocity for 12-mm walleye larvae at 18.3 C was 4.94 cm/sec, compared with 4.0 cm/sec observed at 13 C. Ability of 12-mm yellow perch larvae was estimated at 5.13 cm/sec

for 18.3 C, compared with 4.15 cm/sec observed at 13 C. The estimated velocity agreed well with 1966 data, available only for walleyes, which was 5.0 cm/sec for sustained swimming ability. Lake temperatures reached 15 C when larvae were 12 mm. Sustained swimming velocities at 15 C, estimated from the Q_{10} relation, were only slightly higher than the observed velocities in 1967 at 13 C, being 4.3 cm/sec for walleyes and 4.5 cm/sec for yellow perch. It would have been advantageous to test the sustained swimming of larvae at a series of temperatures, but it was impossible to test enough individuals in the 4-week period during which larvae of the two species were available. The probable importance of temperature on swimming of walleye and perch larvae is suggested by swimming tests on 20–25-mm smallmouth bass, whose swimming ability continued to increase as temperatures were raised to near the lethal limit (Larimore and Duever, 1968).

The 1-hr limit on 1967 swimming tests was assumed to be sufficient time to judge sustained swimming ability. Brett (1964, 1967) has shown that much longer periods were necessary in measuring swimming performances of juvenile sockeye salmon. However, walleye and yellow perch larvae, which swam successfully for 1 hr at a given velocity, were likely to continue swimming for a much longer period, as determined from observations on larvae used in the 1966 tests of 3-hr duration. The commonest response of larvae to a given current velocity was either relatively quick fatigue, or good adjustment and stable swimming throughout the test. Tests that lasted only 10 min in 1966 were not long enough to determine sustained swimming ability.

Young walleye larvae have a relatively greater amount of yolk than yellow perch, and the larger yolk sac probably is responsible for the poorer swimming performance of 7–9-mm walleyes. Swimming ability of 8–9.5-mm walleyes improved quickly during yolk absorption, and both species at lengths from 9.5 to 14 mm swam equally well. However, developmental stages at equal lengths were not the same for the two species. Development of fins and ossification of fin rays takes place at shorter lengths for yellow perch than for walleyes (Norden, 1961). This advantage for yellow perch of a given size is probably balanced by the more developed musculature present in walleyes because of their greater number of postanal myomeres and more robust form.

Sustained swimming ability of walleye and yellow perch larvae was within the 3–4 lengths/sec range suggested by Bainbridge (1960). Larimore and Duever (1968) observed 20–25-mm smallmouth bass swimming at speeds in excess of 10 body lengths/sec for at least 3 min. They suggested that very small fishes may have relatively greater swimming ability than larger individuals of the same species. Results of tests on walleyes and perch indicated that larvae of these species could not sustain currents as great as 10 lengths/sec for even a few minutes. The better swimming ability of young smallmouth bass may reflect the different habitat preference and behavior of this species during its early life. Limnetic larvae, such as perch and walleyes, may depend mostly on drifting for transport, whereas littoral or stream-inhabiting larvae like those of bass may depend more on strong swimming ability.

Distribution of newly hatched walleye and perch larvae in Oneida Lake is not likely to be influenced greatly by swimming ability of either species until they grow to 9.5 mm. Even at this size, the open lake currents are usually much greater than those which larvae could sustain. Lake currents commonly ranged from 4 to 10 cm/sec at depths of 1 m below the surface and were even greater near the surface. Walleye larvae have been found congregated in certain bays of Oneida Lake, and currents within parts of these bays have been demonstrated to be within the range of velocities which larvae longer than 9.0 mm could tolerate. Although walleye and yellow perch larvae both have the ability to maintain themselves within certain parts of these bays, only walleyes are found there, presumably because of differences in behavior of the two species (Houde, 1969).

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NOTES

Atlantic Salmon Returning for Their Fifth and Sixth Consecutive Spawning Trips

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DUCHARME, L. J. A. 1969. Atlantic salmon returning for their fifth and sixth consecutive spawning trips. J. Fish. Res. Bd. Canada 26: 1661–1664.

Six female Atlantic salmon (*Salmo salar* L.) were captured in Big Salmon River, New Brunswick, in August and September 1967. Examination of the scales revealed that four of these fish had spawned four times and two had spawned five times. All were in fresh water at the time of capture and all had commenced erosion at the margin of their scales. Although many of the previously formed growth rings were destroyed by erosion, enough of the scale patterns were left to permit the interpretation of the life histories of the fish.

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ATLANTIC SALMON (*Salmo salar* L.), unlike the Pacific salmon species, often survive one or more spawning trips. The percentage of salmon that spawn more than once varies widely from river to river and from year to year. Dymond (1963) suggested that the percentage of salmon that spawn more than once may be higher in the western Atlantic than in the eastern Atlantic for reasons not yet fully understood. In eastern Canada, the number of return spawners has been observed to vary from 2 or 3% in some rivers to 34% in others (Calderwood, 1927). The majority of the repeat spawners are female fish; a male Atlantic salmon returning to spawn for a second time is a rarity (Dymond, 1963). Normally, from 5 to 15% of the Atlantic salmon survive one spawning trip; less than 5% survive two and fewer still survive three spawnings. Four-time spawners were reported in Quebec in the Moisie River (Menzies, 1926), the western coast of Newfoundland (Taverner, 1958), and Scotland (Nall, 1933). In western Scotland, a salmon with four spawning marks on its scales was taken in the Add River (Menzies, 1925). The fish was a kelt on capture and was, therefore, presumed to have spawned five times. More recently, White and Medcof (1968) described a five-time spawner from Apple River in Nova Scotia.

In 1964, the Resource Development Branch of the Department of Fisheries of Canada initiated a management program on the Big Salmon River, Saint John County, New Brunswick (Fig. 1) involving obstruction removal and salmon smolt stocking.

The assessment of these management procedures included the examination of salmon scale samples which led to the identification of an unusually large percentage of previously spawned salmon (Table 1).

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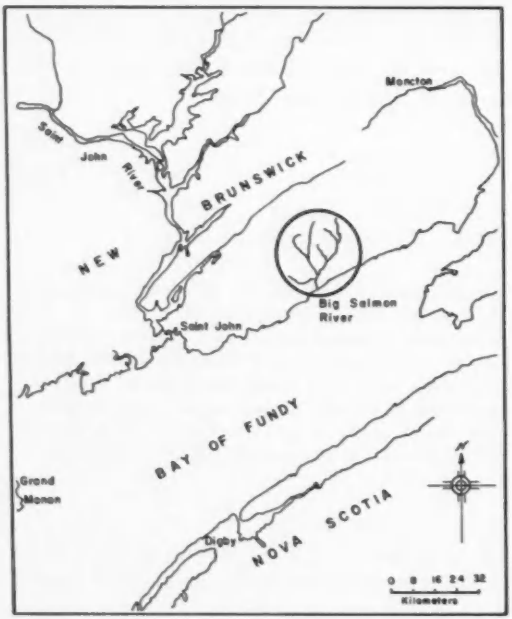

FIG. 1. Location of Big Salmon River, New Brunswick.

TABLE 1. Summary of the spawning history of three samples of Atlantic salmon scales from Big Salmon River, N.B., 1965–67.

Year	No. of fish in sample	Grilse (% sample)	Maiden salmon (% sample)	Previously spawned salmon (% sample)
1965	114	62.3	0.9	36.8
1966	172	69.7	2.3	27.9
1967	169	20.1	17.2	62.7

Nearly all repeat spawners were female fish, 4–7 k in weight. Although the interpretation of the scales of repeat spawners is difficult due to the reabsorption of the hyalodentine layer, the growth patterns on the scales of these fish were remarkably clear, rendering age determination relatively easy.

In 1967, 2475 Atlantic salmon were counted on their ascent to fresh water through a trap at the head of tide. This was a partial count since the trap fence was breached on two occasions by floods. Of these 2475 salmon, 1733 or 69% were fish over 3 k that had spent 2 or more years at sea. The examination of scale samples from 169 fish revealed a salmon to grilse ratio of 3.9:1.0. Only 17% of the large salmon were maiden fish showing 2 and 3 years of saltwater life. Amongst the repeat spawners were four salmon with scales carrying four spawning marks and two with five spawning marks. All had entered fresh water in late summer, a normal occurrence for Big Salmon River fish, and had spawned for their first time as grilse. The scales of the Big Salmon River grilse often include part of a second sea winter (Fig. 2).

FIG. 2. Scale of a typical grilse captured September 5, 1967. Length 55.8 cm.

Ducharme — J. Fish. Res. Bd. Canada

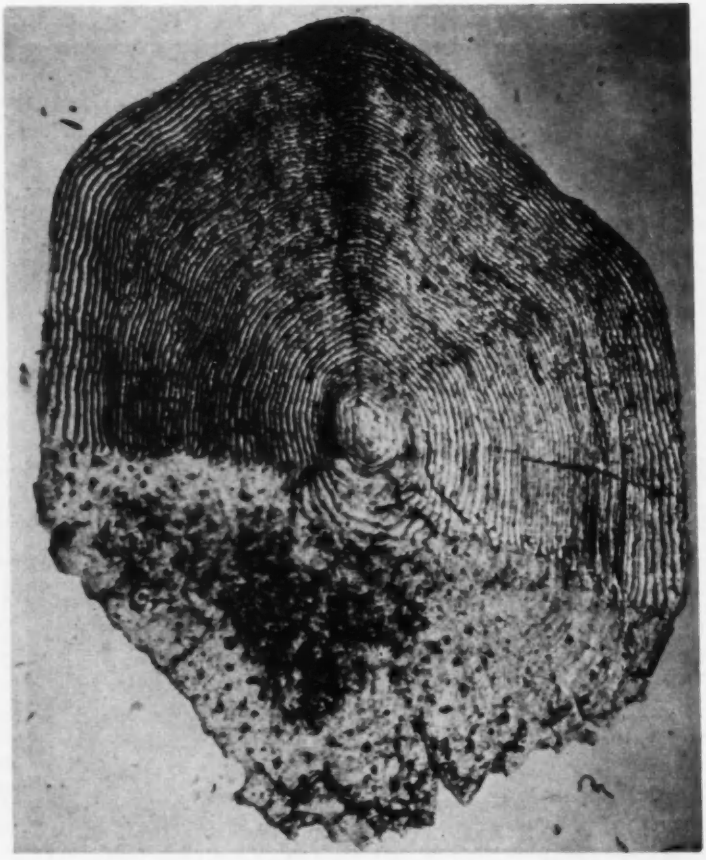

FIG. 3. Scale of a small maiden salmon captured September 2, 1967. Length 76.2 cm.

Ducharme — J. Fish. Res. Bd. Canada

FIG. 4. Scale of a female Atlantic salmon captured September 1, 1967. Length 88.9 cm.

Ducharme — J. Fish. Res. Bd. Canada

FIG. 5. Scale of a female Atlantic salmon captured September 3, 1967. Length 91.4 cm.

Ducharme — J. Fish. Res. Bd. Canada

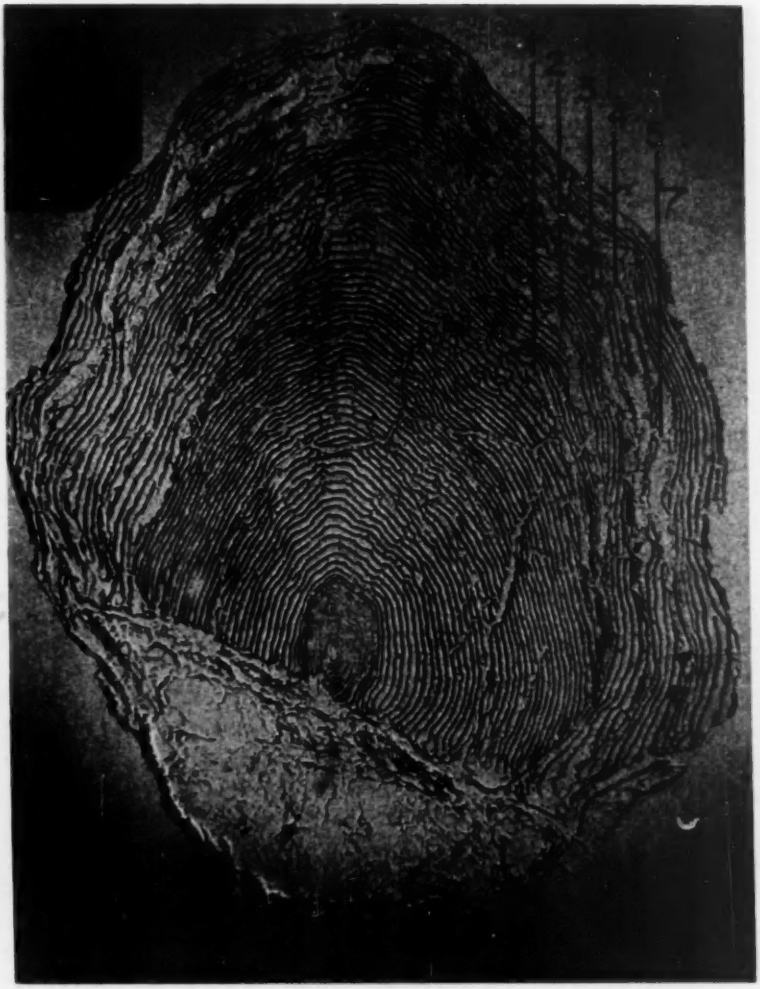

FIG. 6. Scale of a female Atlantic salmon captured August 12, 1967. Length 86.3 cm.

Ducharme — J. Fish. Res. Bd. Canada

FIG. 7. Scale of a female Atlantic salmon captured September 2, 1967. Length 83.8 cm.

Ducharme — J. Fish. Res. Bd. Canada

This pattern would seldom be found, if ever, on the scales of early run grilse. This peculiarity is also noticeable at the scale margin of the 2-sea year salmon (Fig. 3).

In Fig. 4 and 5, the scales show four consecutive spawning marks. Reabsorption is plainly visible at the margin of the scales; this will be the fifth spawning mark should the fish survive. The marks are very distinct from the shoulder down to the posterior end of the scales. Although reabsorption has removed much of the previous summer growth, the eroded areas remain separated by traces of circuli. The anterior end of the scales is relatively free of erosion and thus the annuli are easily identified.

Figure 6 shows a female salmon scale bearing five spawning marks. The fish appears to have first returned to spawn as a grilse and returned every year thereafter. The fish's presence in fresh water, with erosion commencing at the margin of its scales, indicates that it was attempting a sixth spawning trip. The scale shown in Fig. 7 also bears five distinct spawning marks on the dorsal side of the scales. On the ventral side, the last two marks have become fused. This fish was also attempting a sixth trip upriver.

On the whole, reabsorption of the scales of all the fish is somewhat limited. On the anterior portion of the scales it is minimal. This may be partially explained by the fact that these fish entered fresh water in late summer. Menzies (1925) discussed the time of salmon entry in fresh water as a factor limiting the time during which scale absorption will occur. The Big Salmon River fish have a shorter stay in fresh water, hence the call on the resources of the body is reduced. This type of spawning mark formation appears to be typical for Big Salmon River salmon. It permits the scale interpretation of a five-time spawner with a reasonable degree of certainty.

The survival of so many previously spawned fish may be due to the combined effect of a short spawning migration and relatively low angling pressure. Table 2 shows that the anglers removed less than 20% of the total run during the past four years. Normally, in a Maritime salmon stream, well provided with access roads, anglers take from 20 to 40% of the run (Elson and Kerswill, 1964).

TABLE 2. Catches of salmon by angling, Big Salmon River, N.B., 1964–67.

Year	No. counted through trap	Caught By angling	Catch × 100/count
1964	1933	150	7.7
1965	3482	521	15.0
1966	4566	775	17.0
1967	2507[a]	1119	44.5

[a]Incomplete count due to heavy floods.

Also of note is the survival from up to six sojourns at sea. In all probability the Big Salmon River stocks are not being harvested to the fullest extent by the angling fishery and by the commercial fisheries in the Bay of Fundy or further along the northeastern Atlantic coasts. The latter may be an indication that the migration of the Big Salmon River fish is very limited and occurs in areas of relatively light fishing.

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Dichromate Reagent Decomposition and Carbon Estimation

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WESTENHOUSE, RAY G. 1969. Dichromate reagent decomposition and carbon estimation. J. Fish. Res. Bd. Canada 26: 1664–1667.

Potassium dichromate in 33 N H_2SO_4 decomposes to form reduced chromium salts. When the dichromate reagent is stored in clear bottles at room temperature, it decomposes at 3.7% per week; when in amber bottles at room temperature, at 0.62% per week. Dichromate decomposition results in trivalent chromium with the possible liberation of oxygen, as reported by other workers.

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POTASSIUM DICHROMATE in concentrated sulphuric acid has been utilized as an oxidizing reagent for the estimation of carbon in water.

This laboratory has been using the semi-micro (Marshall and Orr, 1964) colorimetric procedure. Particulate carbon is filtered onto glass fiber pads and then oxidized with .05 N $K_2Cr_2O_7$ in 33 N H_2SO_4. Phosphoric acid is used for chloride removal prior to oxidation.

During use of the laboratory-prepared dichromate reagent, we visually observed the color change with storage time. New reagents produced the same results. Absorbance measurements on reagent blanks confirmed the visual observations. A brief literature search disclosed the reagent was thought to be stable (Strickland and Parsons, 1960; Johnson, 1949).

A laboratory study was designed to measure the rate of dichromate decomposition in 33 N sulphuric acid under several storage conditions. Chloride contamination and laboratory cleanliness were initially eliminated as possible causes of decomposition.

Method — Potassium dichromate–sulphuric acid reagent, 0.0509 N $K_2Cr_2O_7$, was prepared from reagent grade chemicals. The final H_2SO_4 concentration was approximately 33 N.

The reagent solution was divided into three volumes and stored in clean glass stoppered bottles as follows:

Bottle	Glass type	Storage	Temp (C)
1	Clear, Pyrex	Open shelf	Room
2	Amber	Open shelf	Room
3	Clear, Pyrex	Refrigerator	4

Each bottle containing the standard reagent was tested weekly to determine if dichromate was stable with time.

Results — Both light and temperature affected the storage stability of dichromate in strong H_2SO_4 (Fig. 1). Light was the dominant factor in the decomposition.

Data on the dichromate stored in the clear bottle at room temperature was evaluated assuming a first order rate law (Daniels and Alberty, 1955), i.e.

$$K = \frac{2.303}{t} \log \frac{Co}{C}$$

where Co = concentration of $K_2Cr_2O_7$ initially present; and C = concentration of $K_2Cr_2O_7$ present at any time t. Approximately 3.7% of the dichromate per week was converted to reduced chromium salts. Analysis of the reagent kept at room temperature in an amber bottle showed a decomposition rate of 0.62% per week. A similar analysis was not performed on the reagent stored in the refrigerator, as these data are clearly not represented by a simple decomposition model. The large change after 18 weeks (Fig. 1) may represent external contamination rather than instability.

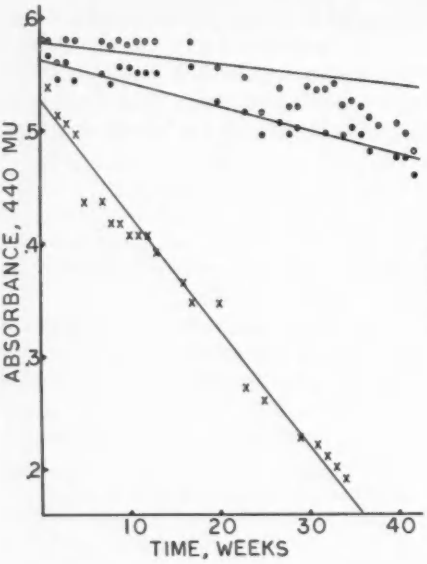

FIG. 1. Decomposition of dichromate in 33 N H_2SO_4. X, clear bottle, on shelf; ●, amber bottle, on shelf; O, clear bottle, in refrigerator. Lines drawn from data analysis by least squares (Hoel, 1958).

Discussion — Epik and Orochko (1958) indicate that $K_2Cr_2O_7$ is decomposed by strong sulphuric acid according to the overall equation

$$2\ Cr_2O_7 = +1\ 6H^+ = 4\ Cr^{+3} + 3O_2 + 8H_2O.$$

They studied decomposition in 16–33 N sulphuric acid. However, from the limited data presented, their work indicates an increasing rate of dichromate decomposition with respect to time and acid concentration. They do not show data for dichromate in 33 N H_2SO_4.

Results of the laboratory rate data indicate the limiting law for dichromate decomposition in concentrated H_2SO_4 may be of the first order. The rate is primarily dependent on the remaining dichromate and photo chemical initiation.

The method, as outlined by Marshall and Orr (1964), does not require an oxidized reagent blank. They recommend a completely reduced reagent blank for instrumental use and assume dichromate–H_2SO_4 reagent stability. Repeated use of their procedure, using nonrefrigerated reagent storage, will result in erroneous estimates of carbon.

To minimize routine test problems when using the dichromate–sulphuric acid reagent, observe the following precautions: (1) store the prepared reagent under refrigeration, preferably in an amber bottle; (2) discard the prepared reagent after 2 months; (3) always determine carbon values (or oxygen) by difference from a reagent blank prepared for each series of samples.

Our experience with this reagent has shown that, with refrigeration, its stability is maintained for 3–4 months. Changes which occur earlier than

2 months have been traced to laboratory cleanliness or chloride carryover in distilled water.

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A Method of Separating Invertebrates from Sediments using Longwave Ultraviolet Light and Fluorescent Dyes

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HAMILTON, ANDREW L. 1969. A method of separating invertebrates from sediments using longwave ultraviolet light and fluorescent dyes. J. Fish. Res. Bd. Canada 26: 1667–1672.

The suitability of nine different fluorescent dyes for selectively staining invertebrates in fresh and formalin-preserved sediments was evaluated. Rhodamine B was the most suitable and tap water was found to be a satisfactory solvent for the dye when fresh samples were being treated, whereas 70 and 95% ethanol were more suitable solvents when the dye was used on formalin-preserved samples. Most invertebrates stained a bright pink and fluoresced a brilliant orange under longwave ultraviolet light. In contrast silt, sand, and most other unwanted components in the sample fluoresced very little if at all. Sorting trials indicated that the use of this method often reduced the sorting time to about one-third of that required when the samples were sorted under visible light. This was particularly apparent when the organisms were small and the samples contained large amounts of sediment and debris.

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THE SEPARATION of invertebrates from sediments represents one of the most tedious, unrewarding, and time-consuming tasks encountered by the aquatic biologist. Most of the methods currently in use involve sieving the sample and picking the specimens from the sieve residue. Frequently the effort involved can be substantially reduced by using one of a number of floatation systems to float the organisms off from the remainder of the sediments. A different approach was followed by Mason and Yevich (1967) and Kořínková and Sigmund (1968) who reported that they could significantly reduce the time required to sort benthic samples by first treating the sieve residue with various dyes and then examining it under visible light. Since this approach seemed to warrant further investigation the following series of evaluation tests was conducted. Only fluorescent dyes were used because any differential uptake of the dye would be exaggerated when the residue was exposed to ultraviolet light.

Materials and methods — Eight fluorescent dyes were used to prepare a total of 18 solutions (Table 1). A fresh sieve residue and a washed formalin-preserved residue were then stained for 20–40 min in each of the solutions. In a few instances additional samples were stained for periods ranging from 5 min to 36 hr. The stained residues were washed thoroughly with tap water before being examined under fluorescent room lighting, and then under longwave (occasionally shortwave as well) ultraviolet light. The fresh sieve residues tested included two small samples of terrestrial top soil stained with a concentration of 0.1% rhodamine B in tap water.

A variety of ultraviolet sources was used including a chromatogram viewer (Fisher Catalogue No. 5-719-600V2) with both a shortwave and a longwave ultraviolet lamp, a separate small longwave ultraviolet lamp (Blak-Ray model X4 with 4-w bulb), and a separate large longwave ultraviolet lamp (Blak-Ray model B 100 with 100-w bulb). Several sorting pans were used including some with black and some with white bottoms. Staining and washing containers were constructed from polystyrene jars and boxes which had the bottoms removed and replaced with "Nitex" monofilament nylon screen. The nylon mesh was bonded to the polystyrene with polystyrene model cement.

Three different persons participated in the trials designed to measure their rates of sorting stained and unstained residues. In the first phase of these tests an unstained sample that had been preserved in formalin was placed in a white enamel pan and examined under visible light. The sorter was provided with a pair of forceps and requested to pick organisms for a specified time limit. The picked organisms were counted and then mixed into the sample for the next trial. After the trials on unstained residues these residues were stained with rhodamine B at concentrations of either 0.1% in tap water or 0.1% in 70% ethanol and the organisms were picked out using the chromatogram viewer and longwave illumination or the small longwave (Blak-Ray model X4) ultraviolet lamp. A second type of test was conducted on a formalin-preserved sample containing a number of very small organisms and much debris. The sample was examined under visible light in a large (20 × 35 cm) white pan and a dissecting microscope was used whenever more detailed examination was required. In this instance the sorters were requested to sort the sample until they would, for practical purposes, consider the process completed. The organisms were counted and then reintroduced into the samples for the next trial. After the control trials the samples were stained with 0.1% rhodamine B in 70% ethanol and the organisms were picked directly from a small (6.5 × 21.5 cm) washing dish set inside a larger black-bottomed pan containing about 1 cm of water. The small longwave ultraviolet lamp was used to illuminate the sample and the sorters were allowed only one-third as much time as they had used on the untreated sample.

Results — The results of the initial series of tests are summarized in Table 1. Rhodamine B proved to be the most suitable for differentially staining invertebrates in sieve residues. All the fresh and preserved Mollusca, Crustacea, and Annelida that were tested stained a bright pink and had a brilliant orange

TABLE 1. The suitability of various fluorescent dyes for differentially staining organisms in sieve residues prior to sorting; E = excellent, VG = very good, G = good, F = fair, P = poor.

Dye solution					Fresh sample		Formalin-preserved sample	
Dye	Supplier	Lot no.	Concn %	Solvent	Visible light	UV light	Visible light	UV light
Rhodamine B	Allied	436P	0.1	70% ethanol	F	F	G	E
" "	"	"	0.5	70% ethanol	F	F	G	E
" "	"	"	0.1	95% ethanol	F	F	G	E
" "	"	"	0.1	Tap water	G	VG	G	VG
" "	"	"	0.5	Tap water	G	VG	G	VG
Uranine	Fisher	770211	0.1	70% ethanol	P	P	F	G
Uranine	Fisher	770211	0.1	Tap water	P	P	P	P
Eosin B	Allied	Neb36	0.1	70% ethanol	P	P	F	F
Eosin B	Allied	Neb36	0.1	Tap water	P	P	P	P
Eosin Y	Fisher	763359	0.1	70% ethanol	P	P	P	F
Eosin Y	Fisher	763359	0.1	Tap water	P	P	P	P
Erythrosin B	Fisher	721563	0.1	70% ethanol	P	P	F	F
Erythrosin B	Fisher	721563	0.1	Tap water	P	P	P	P
Acridine orange	Fisher	753786	0.1	70% ethanol	P	P	F	F
Acridine orange	Fisher	753786	0.1	Tap water	P	P	P	P
Rose Bengal	Fisher	724158	0.1	70% ethanol	P	P	P	P
Rose Bengal	Fisher	724158	0.1	Tap water	P	P	P	P
Phloxine B	Fisher	760166	0.2	95% ethanol	P	P	F	F

fluorescence under longwave ultraviolet light. Formalin-preserved Nematoda stained reasonably well but small live terrestrial nematodes did not take up the stain. The Insecta were somewhat more variable with the Diptera and Ephemeroptera staining very well, whereas there was no external evidence that Hemiptera took up any of the stain. The Odonata and Sialidae were intermediate. Unwanted components of the residue including silt, sand, gravel, and partly decomposed plant or animal material did not stain. Fresh wood chips and nodes of fresh aquatic plants were the only major components of the residue that took up enough stain to cause any difficulties. The short

test performed on fresh terrestrial top soil showed that a variety of terrestrial invertebrates fluoresce very well after treatment in the rhodamine B dissolved in water.

Longwave ultraviolet light caused the stained material to fluoresce much more brightly than shortwave ultraviolet light and the best contrast resulted when the sample was viewed while still in the mesh-bottomed dish used for washing the sample or when it was placed on a black background and covered with little or no water. A minimum of 20 min was required to stain the samples satisfactorily and extending the staining time to up to 36 hr did not appear to alter the result. Organisms that were improperly preserved in too low a concentration of formalin would not take up the stain properly and even well-preserved samples could not be stained by adding dye directly to the formalin solution. Before staining it was essential to wash such samples for at least 5 min to get rid of the excess formalin. The best contrast was achieved when a strong longwave ultraviolet source was used, and the fluorescence was observed through a filter that removed the ultraviolet and blue parts of the spectrum, thus eliminating some of the wavelengths that are most irritating to the eyes.

Rhodamine B dissolved in tap water was most suitable for staining fresh samples, whereas ethanol was a more suitable solvent when the samples had been preserved in formalin. The uptake of dye by specimens that had been preserved in formalin was apparently unrelated to the solvent used but after washing there was considerably more leeching of the dye from those samples where tap water was used as the solvent.

The results of the time trials were quite variable although in every instance more organisms were picked from the stained samples viewed under longwave ultraviolet light. The organisms picked from the unstained sample using visible light expressed as an average percentage of those picked from the stained sample ranged from 78% on a very clean sample to only 30% on a sample containing considerable debris and very few organisms. The results of the second experiment where a sample containing about 20 cc of residue was first sorted normally and then in one-third the time after treatment are summarized in Table 2. The number of organisms picked in the different trials was essentially the same.

Discussion — A number of the dyes examined in this series of tests could be of some use in the separation of invertebrates from sediments; however, rhodamine B is definitely the most promising. It is taken up by almost all the living or formalin-preserved organisms found in freshwater sediments while at the same time it is not taken up by sediments or partly decomposed plant material. As a result it is particularly well suited for use with samples containing a large amount of sediments and plant debris. The trials conducted indicate that the sorting time for such samples can be cut to a third or less by staining with rhodamine B and then examining the samples under longwave ultraviolet light. In addition it seems certain that had a larger washing dish

TABLE 2. Results of sorting trials on a formalin-preserved sample illuminated first with visible light before staining and then with longwave ultraviolet light after staining with 0.1% rhodamine B in 70% ethanol.

Sorter	Sorting time (*min*)	Illumination	Sphaeriids	Ostracods	Chironomids	Ceratopogonids	Total
1	54	Visible light	–	–	28	–	28
1	18	Longwave UV	–	2	34	1	37
2	60	Visible light	1	3	32	–	36
2	20	Longwave UV	–	2	29	1	32
Actual no. in sample			1	3	44	1	49

been available, similar in size to the white pan used with the untreated samples, the results would have been even more dramatic because the residue would have been spread much thinner. On the other hand the method will not likely result in much of a reduction in the sorting time on relatively clean samples unless small, rather transparent organisms such as ostracods, copepods, or early instar chironomids are being collected. The same generalizations probably apply equally well to terrestrial samples. The apparent relationship between the state of decomposition of organic material and the amount of dye taken up by it could prove useful for detecting living material particularly if the relationship holds for phytoplankton and the nonmotile stages of invertebrates.

The major shortcoming of rhodamine B as an agent for differentially staining sieve residues is that after the stained samples are washed there is still some leeching of the dye into the surrounding water. The problem is more serious when water is used as the solvent for rhodamine B but it occurs to some extent with all solutions. It can be almost completely eliminated by constructing the sorting pan so that a small amount of water continues flowing through the sample while the sorting is in progress. None of the ultraviolet equipment available was ideally suited to this type of testing program; however, it would not be difficult to build a viewing box equipped with longwave ultraviolet lights and constructed so that the sample could be observed from close range through a filter that removed the blue and ultraviolet parts of the spectrum.

Acknowledgments — Several people at the Freshwater Institute, Fisheries Research Board of Canada, Winnipeg, Man., contributed significantly to this experiment. Dr D. P. Scott provided much of the material and equipment. He also offered many pertinent suggestions, particularly in relation to the actions of various fluorescent dyes. Dr K. Patalas contributed a number of ideas and brought one of the papers that led to the initiation of this experiment to my attention.

I would also like to thank Mr G. P. McRae who assisted with a number of technical aspects of the experiment.

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Aggregations of Spottail Shiners and Yellow Perch

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Spottail shiners (*Notropis hudsonius* (Clinton)) and immature yellow perch (*Perca fluviatilis* Linnaeus), ranging in size from 30 to 110 mm, total length, aggregate in shallow water in Beaver Lake, Alberta. The ratio of number of shiners to that of perch is about 1.5:1. Perch larger than 110 mm leave the aggregation. Eventually they will prey on it from below. Other predators include northern pike and walleye, which lie below the aggregation, and terns and gulls from above. Shiners in the aggregation are 10 times more likely to be taken by fish predators than are perch.

Received January 10, 1969

CASUAL OBSERVATIONS from the float-plane dock of the Alberta Forest Service at Beaver Lake, Alberta (54°45′N, 111°50′), showed that spottail shiners (*Notropis hudsonius* (Clinton)) and immature yellow perch (*Perca fluviatilis* Linnaeus) commonly aggregated in shallow water. Collections and observations were made during the period June 14–19, 1968, to elucidate further the nature of the aggregation. Aggregations of the sort observed could be called schools, under the definition of Keenleyside (1955), which is that a school is "an aggregation formed when one fish reacts to one or more other fish by staying near them." However, because of the bispecific nature of these aggregations, we prefer not to use the term *school*.

The Forest Service dock is L-shaped. The dock is on piles, so that on all sides there is free access to the open lake. The area enclosed by the shore and the arms of the dock provided a useful reference area for repetitive observation and collection. Within the area the water depth increases gradually

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to about 5 m at the outer limit of the enclosure. Conditions within the enclosure were much the same as in other littoral areas of the lake.

The fish were sampled by means of seine hauls (10 × 1.5 m, 0.5 cm mesh) at the dock; they were further observed by means of snorkel and scuba gear there and in neighboring littoral areas, and at a central shoal in Beaver Lake. The aggregations are abundant and widespread.

Beaver Lake is 14.4 km long and 2.8 km wide. It has an area of 33 km², and a shore development of 4.18. Its maximum depth is 15.2 m and mean depth 6.9 m. It has the following species of fish: *Coregonus clupeaformis* (Mitchill) (lake whitefish), *Esox lucius* Linnaeus (northern pike), *Notropis hudsonius* (Clinton) (spottail shiner), *Catostomus commersoni* (Lacépède) (white sucker), *Lota lota* Linnaeus (burbot), *Etheostoma exile* (Girard) (Iowa darter), *Stizostedion vitreum* (Mitchill) (walleye), *Perca fluviatilis* Linnaeus (yellow perch).

Table 1 illustrates the composition of aggregations as shown by three seine hauls taken at different times of day. Haul no. 3 confirms the visual observation that the aggregations disperse at night.

TABLE 1. Composition of spottail shiner–yellow perch aggregations as shown by seine hauls.

Haul no.	Date (*1968*)	Time	No. shiners	No. perch	No. shiners: perch
1	June 14	5:00 PM	5259	3358	1.57
2	16	11:00 AM	9338	6205	1.50
3	17	10:30 PM	36	29	1.24

The size ranges of the aggregating fish were: spottail shiner 30–105 mm; yellow perch 48–110 mm, total length.

An aggregation takes a definite position in the water (Fig. 1). Generally the uppermost fish are about 15–20 cm below the water surface. The lowest fish of the aggregation swim 30–50 cm above the bottom, in water 1–3 m deep. An aggregation is more related to the water surface than the lake bottom; the distance of the aggregation from the bottom is greater in deeper water.

Within the aggregation, there is a size/depth stratification, with smaller fish tending to stay near the top and larger individuals more common near the bottom. The relationship between individual size and position in the aggregation is more marked in the spottail shiner than in the yellow perch. The perch are more uniform in size than the shiners; only at the bottom of the aggregation was there any clear relationship between perch size and behavior. There, as they reach the maximum size for individuals in the aggregation (about 110 mm), the perch begin to drop out of the aggregation.

There is also a tendency towards species stratification, the spottail shiners being more abundant in the upper layers of the aggregation, the perch concentrating in the lower. Both these types of stratification are definite, but not fixed. Fish of all sizes can be found at all levels, and there is a broad zone of intermingling of the two species.

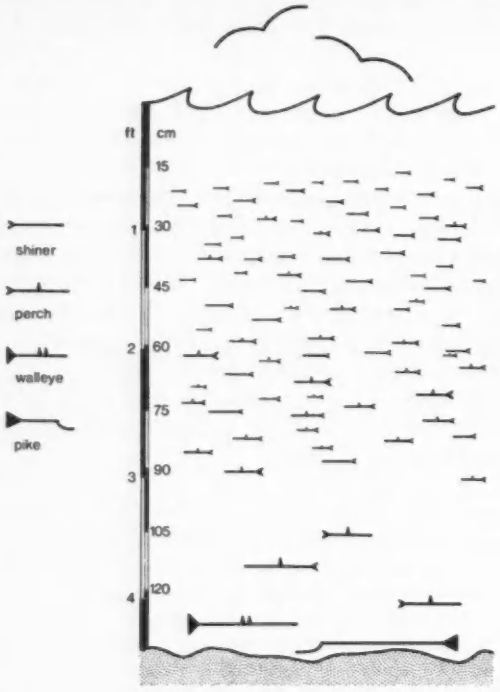

FIG. 1. A common organization for a spottail shiner–yellow perch aggregation in shallow water. The orientation of the individuals is generally much more diverse than illustrated; the dimensions of the page limit the graphic representation. Note predatory birds above and predatory fish below.

Some aggregations are made up entirely of spottail shiners. Fewer perch occur in aggregations in water deeper than about 6 m. Aggregations of small perch alone were not seen.

Both shiners and perch are present in literally countless numbers. We think that the shiners are much more abundant than the perch and form the basis of the aggregations; small perch take advantage of the presence of aggregations and join them, often in large numbers. Deelder (1951) noted that 70–90-mm perch tended to aggregate with roach.

One hundred spottail shiners and 52 yellow perch from an aggregation were examined for qualitative stomach content comparison. As would be expected, there was much similarity in the stomach contents of aggregating shiners and perch. But there were also significant differences.

Major food items for both species were Cladocera (especially *Daphnia retrocurva* Forbes) and Copepoda (*Cyclops* sp. and *Diaptomus* sp.).

Perch in the aggregations depended chiefly on pelagic prey, e.g., chironomid pupae, mayfly nymphs, *Leptodora kindtii* (Focke), as well as the cladocerans mentioned above. Larger perch in the aggregations ate *Hyalella azteca* (Saussure).

The shiners ranged more widely in their feeding. As well as feeding on plankton throughout the water column, they often fed at the surface, as

illustrated by the presence of daphniid ephippia, pollen, and ectoproct statoblasts in their stomachs, and also in surface plankton tows. Shiners also fed at the bottom; chironomid larvae were common in their stomach contents.

The data of the previous paragraphs provide a qualitative basis for our observations that shiners will rise to the surface in calm weather and will descend to the bottom in shallows, while the perch appear to maintain position in midwater.

During their surface-feeding activities the shiners were particularly subject to predation by birds, especially the common tern (*Sterna hirundo* Linnaeus), and also the black tern (*Chlidonias niger* (Gmelin)) and the California and ring-billed gulls (*Larus californicus* Lawrence and *L. delawarensis* Ord). At almost all times these birds could be observed fishing. Even when the aggregation stays well below the surface, wanderers above it are subject to capture.

The space beneath the aggregation, between it and the bottom, is also important. Perch, northern pike, and walleye are common there (Fig. 1). All these species prey on individuals from the aggregation.

The perch beneath the aggregation range in size from just above the aggregation maximum (about 105–110 mm) to full-sized adults. The larger the fish, the closer to the bottom it swims. Although not aggregated, the larger perch exhibit some gregariousness. Often three or four individuals are close together, within 6 inches or so of one another. They tend to swim together. If disturbed, they disperse in different directions. Where we were observing, the perch, brilliantly striped and colored, were quite obvious. The aggregations did not seem to be disturbed by them.

Northern pike are also present beneath the aggregations. In shallow water, the pike are usually in the 20–50-cm size range, but much larger pike also appear. The pike are solitary. They stay very close to the bottom. They swim slowly and often come to rest on the bottom, to lie motionless for minutes at a time. They are extremely difficult to see. An aggregation reacts much more negatively to a moving pike than to a moving perch, by those fish nearest the predator darting away from it.

Walleye are less common. They move fairly rapidly through the space beneath the aggregation, close to the bottom. We did not observe any special disturbance of an aggregation by the presence of walleye. Perhaps sudden movement, as by a pike after lying motionless, is more disturbing to the aggregated fish than a continued passage by a predator, even though it be nearby.

The nonaggregating perch had a varied diet, including amphipods, chironomid larvae and pupae, shiners, a variety of aquatic insects, snails, and leeches. The pike and walleye sampled from beneath the aggregations had been feeding exclusively on shiners and perch of aggregation size, in the ratio of about 10:1.

The chief significance of these observations is that in Beaver Lake it is common for such apparently unlikely combinants as spottail shiners and yellow perch to aggregate intimately, at least while the perch are of a similar

size to the shiners. Polytypic aggregations are not unknown, but they are uncommon. An example of such an aggregation is reported by Breder (1959) between *Notemigonus crysoleucas* (Mitchill) and *Erimyzon sucetta* (Lacépède), but it does not represent a grouping of potential predators and prey as the spottail shiner–yellow perch aggregation does.

This note is a report of the phenomenon. It is intended that further examples will be sought in other Alberta lakes, and that closer analysis in behavioral terms will follow.

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Relations between Length of the Pen and Other Measurements in the Squid *Lolliguncula brevis*[1]

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DRAGOVICH, ALEXANDER, AND JOHN P. WISE. 1969. Relations between length of the pen and other measurements in the squid *Lolliguncula brevis*. J. Fish. Res. Bd. Canada 26: 1676–1679.

The relations between length of the pen and other measurements in the squid *Lolliguncula brevis* were studied to estimate the volume of partially digested squid recovered from tuna stomachs. Relations between the pen length and mantle length and between pen length and volume were analyzed by regression. Conversion tables were constructed on the basis of these analyses to estimate the original volume of the squid from the length of the pen.

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THE CHIEF FUNCTION of the research at the Tropical Atlantic Biological Laboratory is the study of the biology and ecology of tunas of the tropical Atlantic Ocean. Because our research on food and feeding habits of tunas

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involves not only the species composition of tuna food but also its nutritive value, it is necessary to estimate the volumes of food items found in tuna stomachs. Food organisms from stomachs are often damaged by digestive processes; therefore, methods must be devised for estimating the original volumes of forage organisms. The more durable parts of an organism may form the basis for useful measurements.

Squid pens (*gladii*) are more resistant to digestion than any other part of the body except the beak. In many instances intact gladii are found in partially digested squid in the stomachs of tunas. We have, therefore, analyzed the relations between pen length, mantle length, and displacement volume for a stratified sample of *Lolliguncula brevis* (Blainville).

Lolliguncula brevis is a shallow-water euryhaline squid, known from the Bermuda Islands, Atlantic coast of the United States from Maryland to Florida, Gulf of Mexico, Caribbean Sea, and South America to Rio de la Plata (Voss, 1956; Dragovich and Kelly, 1967). This squid is important in the diet of many fishes as well as in the diet of *Thunnus atlanticus* (blackfin tuna) and *Katsuwonus pelamis* (skipjack tuna) in Cuban waters (Suarez C. and Duarte B., 1961), and also has been recorded from the stomachs of *Euthynnus alletteratus* (little tuna) from the northern Gulf of Mexico. Some aspects of morphometry of *L. brevis* have been studied by Haefner (1964).

A stratified sample of *L. brevis* was taken from a collection of over 1000 *L. brevis* taken in Tampa Bay, Florida, and in the adjacent Gulf of Mexico, and preserved in 60% isopropyl alcohol. When possible, 10 squid of each 1-cm group of mantle length were measured. We took the body length of the squid as equivalent to the mantle length, measured from the anterior tip of the mantle to the posterior end of the mantle.

We measured 83 specimens, distributed as follows: 10 each in the 1.1–2.0 through 7.1–8.0-cm groups; 9 in the 8.1–9.0-cm group; and 4 outside these ranges (1.0, 9.2, 10.0, and 10.2 cm). Squid less than 1.8 cm (11 specimens) were not sexed since the sex at this length is difficult to determine; of the other 72 squid, 54 were females and 18 were males. Males appeared randomly distributed among the length groups.

We determined the displacement volume of each squid to the nearest 0.1 ml, using Thrailkill's (1957) method. We then measured the mantle length, removed the dorsal mantle, and measured the pen. All linear measurements were taken with vernier calipers and recorded to the nearest 0.1 mm.

Relations between pen length and mantle length and between pen length and volume were analyzed by regression. As might be expected, the lengths of the pen and the mantle are closely related. When P is taken as pen length and M as mantle length, both in millimeters, the relation used was:

$$M = a + b\,P.$$

TABLE 1. *Loliguncula brevis*: relations among various measurements.

Pen length (*mm*)	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95	100	105	110
Mantle length (*mm*)	11	16	21	26	31	36	41	46	51	56	61	66	71	76	81	86	91	96	101	106	111
Volume (*ml*)	0.2	0.4	1	1	2	3	5	6	8	10	13	16	19	23	27	31	36	41	47	53	59

The line for this equation was fitted to various subsamples (r = coefficient of correlation; df = degrees of freedom):

	a	b	r	df
Males	2.311	0.992	0.995	16
Females	1.624	1.000	0.997	52
Not sexed	1.581	0.935	0.962	9
All combined	1.174	0.998	0.998	81

Solutions for the equation, based on combined values, are given in Table 1.

When P is pen length in millimeters and V is the displacement volume in milliliters the relation is:

$$\log V = a + b \log P.$$

The line for this equation was fitted to various subsamples:

	a	b	r	df
Males	−3.497	2.591	0.994	16
Females	−3.569	2.641	0.992	52
Not sexed	–	–	–	–
All combined	−3.315	2.493	0.991	81

No significant correlation was found between log P and log V for the nonsexed individuals in the sample, probably because the series was not long enough. Solutions for the logarithmic equation, based on combined values, are given in Table 1.

Development of similar conversion tables for other invertebrates and fishes will be helpful in studies of food habits, as well as in other biological investigations.

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First Records from the Northeastern Pacific of the Deep-Sea Ophidioid Fish *Parabassogigas grandis*

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EAGLE, RODNEY J. 1969. First records from the northeastern Pacific of the deep-sea ophidioid fish *Parabassogigas grandis*. J. Fish. Res. Bd. Canada 26: 1680–1685.

Seven specimens of *Parabassogigas grandis* previously reported off Japan have been captured in deep water off Oregon. Morphological variation due to growth is discussed, and additional descriptive data are given.

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SINCE 1965 seven specimens of the rare deep-sea fish *Parabassogigas grandis* (Günther) have been captured in otter trawls on the continental slope (2130 m) and abyssal plain (2800 m) off Oregon. This species was formerly known from only two specimens collected off Japan (Günther, 1877; and Tanaka, 1908). Table 1 summarizes the collection data for *P. grandis* captured off Oregon and Japan. The known range of this species is now extended to the northeastern subarctic Pacific Ocean. The new records also modify the known bathymetric range for this species to 2130–3430 m.

According to Nybelin (1957), the genus *Parabassogigas*, which is represented in the Atlantic by *P. crassus* (Vaillant) and the Pacific by *P. grandis*,

TABLE 1. Collection information for *Parabassogigas grandis*, including the seven specimens captured by Oregon State University Department of Oceanography (OSUDO).

Collection	Date	Location	Lat	Long	Depth (*m*)
Günther	1877	Western Pacific off Yokahama	34°37′	140°32′	3430
Tanaka	1908	Western Pacific off Yokahama	34	140	Unknown
OSUDO 1352	Jan. 12, 1965	NE Pacific, 65 miles off Newport, Ore.	44 40	125 35	2800
USNM No. 199273	Jan. 12, 1965	NE Pacific, 65 miles off Newport, Ore.	44 40	125 35	2800
OSUDO 1353	Aug. 21, 1965	NE Pacific, 85 miles off Newport, Ore.	44 40	126 0	2800
OSUDO 1354	Aug. 21, 1965	NE Pacific, 85 miles off Newport, Ore.	44 40	126 0	2800
OSUDO 1355	Oct. 15, 1966	NE Pacific, 65 miles off Newport, Ore.	44 40	125 35	2800
OSUDO 1356	Jan. 11, 1967	NE Pacific, 55 miles off Tillamook, Ore.	45 45	125 30	2130
OSUDO 1526	Oct. 29, 1967	NE Pacific, 65 miles off Newport, Ore.	44 49	125 35	2800

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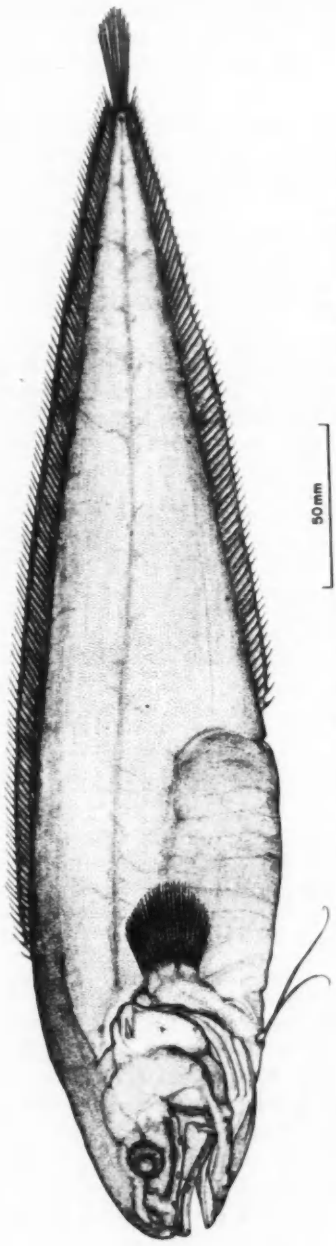


FIG. 1. *Parabassogigas grandis* (Günther). Specimen OSUDO No. 1354, 351 mm long (scales are not shown).

TABLE 2. Meristic and morphometric comparisons of *Parabassogigas grandis*. Parentheses indicate body proportion in per cent of standard length.

Character	Günther, 1877 type[a]	Tanaka, 1908	OSUDO 1352	OSUDO 1353	USNM 199273	OSUDO 1354	OSUDO 1355	OSUDO 1356	OSUDO 1526
Standard length (mm):	673	1175	1090	780	445	351	450	469	424
Body: depth at vent	131(19.46)	163(13.87)	240(22.02)	168(21.53)	–	75(21.37)	79(17.56)	82(17.48)	86(20.28)
Head: length	146(21.65)	235(20.00)	215(19.60)	163(20.85)	99(22.10)	73(20.65)	92(20.44)	94(20.04)	94(22.17)
Snout: length	21(3.12)	58(4.95)	56(5.12)	48(6.16)	23(5.16)	17(3.32)	26(5.78)	27(5.76)	22(5.19)
Eye: diam	15.5(2.31)	22.0(1.87)	20.0(1.83)	18.0(2.31)	14.0(3.15)	11.0(3.13)	13.0(2.89)	13.0(2.77)	13.0(3.07)
Interorbital: width	–	54(4.60)	76(6.96)	54(6.94)	29(6.51)	22(6.25)	30(6.67)	31(6.61)	29(6.84)
Maxilla: length	–	126(10.72)	114(10.48)	85(10.90)	41(9.20)	31(9.68)	40(8.89)	39(8.32)	36(8.49)
Premaxilla: length	–	–	116(10.64)	87(11.15)	47(10.36)	34(9.69)	45(10.00)	45(9.59)	46(10.85)
Lateral line: length	–	–	215(19.72)	95(12.18)	53(11.91)	34(9.69)	44(9.78)	51(10.87)	30(7.08)
Outer ventral ray: length	–	–	61(5.60)	45(5.77)	36(8.09)	31(8.83)	39(8.67)	40(8.53)	36(8.49)
Inner ventral ray: length	81.6(12.12)	125(9.90)	102(9.35)	75(9.65)	55(12.35)	52(14.85)	69(15.33)	67.5(14.39)	62(14.62)
Snout to dorsal	–	–	302(27.71)	220(28.21)	135(30.34)	95(27.07)	121(26.89)	140(29.85)	123(29.01)
Snout to anus	315(46.90)	440(37.50)	460(42.20)	370(47.40)	210(47.20)	143(45.30)	194(43.11)	195(41.58)	192(45.28)
Snout to base of ventrals	–	–	155(14.22)	150(19.23)	–	52(14.81)	65(14.44)	70(14.92)	62(14.62)
Snout to rear of maxilla	65(9.66)	–	112(10.28)	85(10.90)	–	34(9.69)	50(11.11)	49(10.48)	48(11.32)
Base of pectorals to anus	–	–	235(21.56)	196(24.37)	105(23.60)	76(21.65)	99(22.00)	100(21.32)	99(23.35)
Base of ventrals to anus	–	–	345(31.65)	215(27.56)	145(32.58)	103(29.34)	132(29.33)	127(27.08)	135(31.84)
Pectoral length	65(9.66)	116(9.87)	92(8.44)	68(8.72)	42(9.94)	35(9.97)	44(9.78)	45(9.59)	46(10.85)
Space between nostrils	–	–	12(1.10)	10(1.28)	8.0(1.80)	5.0(1.42)	8.0(1.78)	6.5(1.39)	6.0(1.42)
Distance between base of ventrals	9.2(1.37)	–	18(1.65)	10(1.28)	–	5.5(1.56)	6.0(1.33)	6.5(1.38)	6.0(1.42)
Rays in dorsal	–	140	139	131	115	113	121	117	120
Rays in anal	–	106	106	104	85	73	84	92	89
Rays in pectoral	29	28	30	29	29	29	26	27	26
Gill rakers (first arch)	–	3 or 4+8	3+8	3+8	–	3+9	4+8	4+8	–
Sex	–	–	Male	Female	Female	Female	Female	Male	Female

[a]Measurements taken by Dr Daniel Cohen, U.S. National Museum (personal communication).

is distinguished from closely related genera (*Bassogigas*, *Mastigopterus*) by dentitional characters. The vomerine teeth form a triangular patch, and the basibranchial teeth form two median, unpaired patches — a larger anterior patch and a small posterior patch with no intervening patches.

The *P. grandis* from Oregon (Fig. 1) compare well with the description of the type and Tanaka's specimen. The body proportions of the new records are within 3% or less of the standard length in all morphometric features given for the type specimen (Table 2).

Some characteristics of *P. grandis* either not mentioned or detailed in the preliminary and detailed descriptions (Günther, 1877, 1887), but which may be diagnostically important are as follows:

Lower jaw included; snout, fleshy and rounded. Cephalic pores 11, five on the maxillary sheath, five on the lower edge of the dentary sheath, and one on the preopercle. Small villiform teeth on the jaws, palatines, basibranchials, and vomer. Vomerine patch triangular to broadly triangular (Fig. 2); posterior basibranchial patch oval to bipartate (Fig. 2). Two pairs of nostrils, the anterior ones rounded and produced, the posterior pair a vertical elongate slit. Free edge of

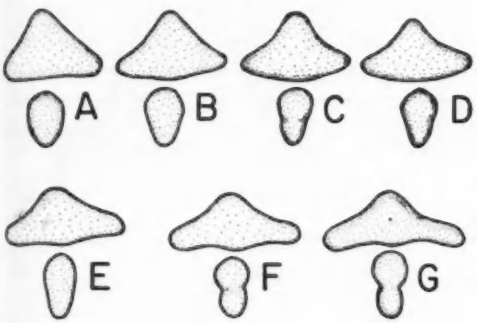


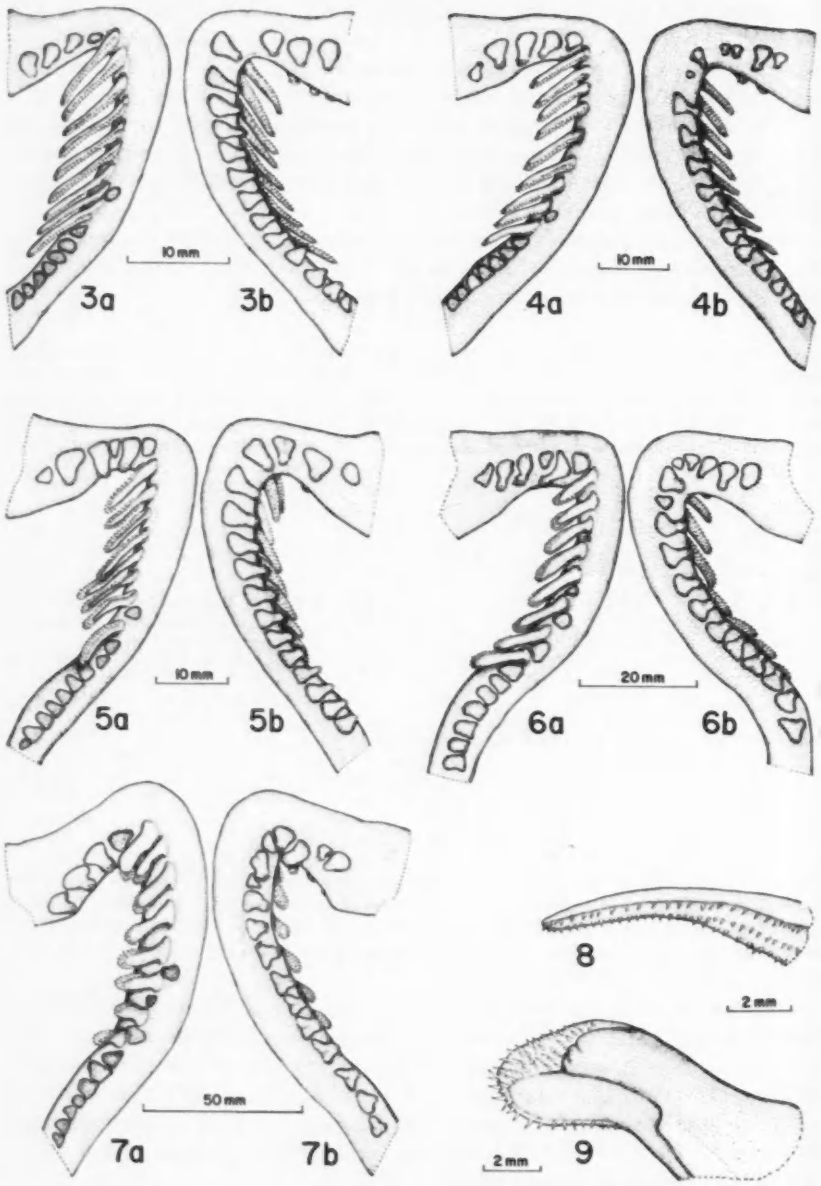
FIG. 2. Sketches of vomerine and posterior basibranchial patches of specimens of *Parabassogigas grandis*: A, 351 mm; B, 445 mm; C, 450 mm; D, 469 mm; E, Nybelin's sketch of type 673 mm; F, 780 mm; G, 1090 mm.

the preopercular fold extends to or slightly above the level of the maxillary sheath. Lateral line conspicuous, reaching to or slightly beyond the origin of the dorsal fin. Three short, blunt gill rakers on the upper arm of the gill arch, one long raker at the angle, and 7–8 rakers, plus 8–9 low pads on the lower arm (Fig. 3). Opercular spine, short, sharp and rounded.

The specimens from Oregon represent a large size range, 351–1090 mm standard length (SL), and show striking differences in eye morphology, dentition, and gill arch structure that are related to size or age. The smallest specimen (351 mm) has relatively large eyes (3.13% of SL) that protrude and have clear corneas. In contrast, the larger fishes (780, 1090 mm) have small eyes (1.83–2.31% of SL) that are recessed and covered with a thick, translucent or opaque corneal tissue.

The shapes of the vomer and posterior basibranchial also progressively change with length. The vomerine patch is bluntly triangular (height 1.43 in length) in the smallest fish and broadly triangulate (height 2.60 in length)

Measurements taken by Dr Daniel Cohen, U.S. National Museum (photo



FIGURES 3–9. Left gill arch of ***Parabassogigas grandis.***

Fig. 3–7. Outer (*a*) and inner (*b*) arches of: Fig. 3. 351 mm (OSUDO 1354); Fig. 4. 450 mm (OSUDO 1355); Fig. 5. 469 mm (OSUDO 1356); Fig. 6. 780 mm (OSUDO 1353); Fig. 7. 1090 mm (OSUDO 1352). Fig. 8 and 9. Angle gill rakers of arches shown in Fig. 3 and 7 respectively.

in the largest fish (Fig. 2). The specimens of intermediate size have intermediate shapes. The basibranchials are oval in the small fish and partially bipartate in the large fish (Fig. 2).

The morphology of the first gill arch, moreover, shows a gradual but obvious change with length (Fig. 3–7). The gill rakers are relatively long (angle raker 2.3% of SL) in the small fish and short (angle raker 1.0% of SL) in the largest fish (Fig. 8, 9). Neither the 424-mm specimen (OSUDO 1526), which was captured while this note was in progress, nor the specimen deposited with the U.S. National Museum is illustrated. Their dentition and gill arch morphometry are similar to those of the 450-mm and 469-mm specimens (OSUDO 1355 and 1356).

No sexual dimorphism is apparent in our specimens other than color. The males are a dusky cream; the females a light grey–brown.

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A New Type of Emergence Trap for Collecting Stream Insects

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The stream emergence trap described in this note collects the insects that emerge from an enclosed area of substrate. It will function at depths exceeding 12 cm and is designed so that as insects leave the enclosed substrate to emerge they are carried by the current to the downstream end of the trap where there is a quiet area in which they can emerge. The sampler proved particularly effective for collecting adult mayflies, caddisflies, and midges along with their cast exuviae. Major advantages of this emergence trap are that it can be emptied quickly and that the specimens are well suited to both taxonomic studies and studies of organism–substrate relationships.

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EMERGENCE TRAPS are essential for the study of emergence patterns of aquatic insects and can also provide semi-quantitative population estimates that are particularly valuable from those areas where conventional substrate samplers will not function. A number of different types have been used including floating funnel traps (Corbet, 1966; Mundie, 1956), partly submerged funnel traps (Mundie, 1956, 1966), and box traps with sides of wire mesh that extend to the bottom of the stream (Ide, 1940; Sprules, 1947). In all these samplers the insects emerge above the stream surface and only the box trap encloses an area of substrate that can be related directly to the insects emerging in the sampler.

The emergence trap (Fig. 1) described in this report operates on a different principle than previously described types designed for use in streams. It collects the emerging adults and their cast exuviae from a specified section of stream substrate and is designed to function while completely submerged. A major advantage of this emergence trap is that the sample can be collected quickly without the aid of an aspirator. In addition the fact that it routinely collects the cast exuviae along with the adults makes the samples considerably more useful for taxonomic purposes.

Details of construction — The sides of the trap (Fig. 2A), the slats (Fig. 2B and C) for the removable screens, and the support braces (Fig. 2D and E) across the bottom of the slats and at the back of the funnel were constructed of $\frac{1}{16}$-inch stainless steel sheeting. The three support rods (Fig. 2F) were $\frac{1}{4}$-inch stainless steel rods with 2 cm of threading at each end so that a nut could be placed on both the inside and outside of each of the side panels. The stakes for holding the trap in position were $\frac{1}{4}$-inch stainless steel rods about 40 cm long, and the flange (Fig. 2G) with a $\frac{3}{8}$-inch hole to take the stake was made from $\frac{1}{8}$-inch stainless steel. The top (Fig. 2H) of the upstream part of the trap, the slats (Fig. 2I and J), which were grooved to take the funnel, and the closing bar (Fig. 2K) which was located behind the funnel, were made of $\frac{1}{4}$-inch perspex. The funnel (Fig. 2L) for the trap was made from 25-mil clear vinyl plastic. The pattern was cut, set over a metal mold, and bent along the fold lines. The bending was facilitated by heating the plastic along the fold lines with a small butane or propane burner. A small electric soldering iron or hobby tool, which also makes an excellent tool for cutting the pattern, was then used to heat-seal the seam. A lip was formed on the funnel by placing the small end in near-boiling water and forcing a glass jar with an outside diameter of 58 mm through the opening. A stainless steel hose clamp (Fig. 2M) was used to attach a 58-mm bakelite lid (Fig. 2N), which had a hole 45 mm in diameter cut out of its center, to the funnel. A 12-oz jar (Fig. 2O), was used as a collecting vessel and was attached to the funnel by means of the 58-mm bakelite lid clamped in the funnel. A strip of $\frac{1}{4} \times \frac{1}{2}$-inch sponge weather stripping (Fig. 2P) was glued on the underside of the posterior lip of the funnel to provide a better seal. The downstream part of the trap, below the last screen, was sealed off with a plate (Fig. 2Q) of 25-mil vinyl plastic. A metal template and a small propane or butane torch were used to bend the anterior lip to 70°. A small vinyl strip (Fig. 2R) bent to about 30° and attached with pliobond glue to the underside of the posterior margin of the perspex served to provide a better seal for the front of the funnel. The removable screens (Fig. 2S) were made of nitex nylon screen (apertures 405 μ sq) heat-sealed or glued with pliobond glue between two vinyl 25-mil plastic frames (Fig. 2T). The trap was assembled with $\frac{1}{4}$ and $1\frac{3}{16}$-inch diam stainless steel bolts.

Operation — These emergence traps have been used in two streams for one season that extended from early May to early October. The models used

FIG. 1. Stream emergence trap.

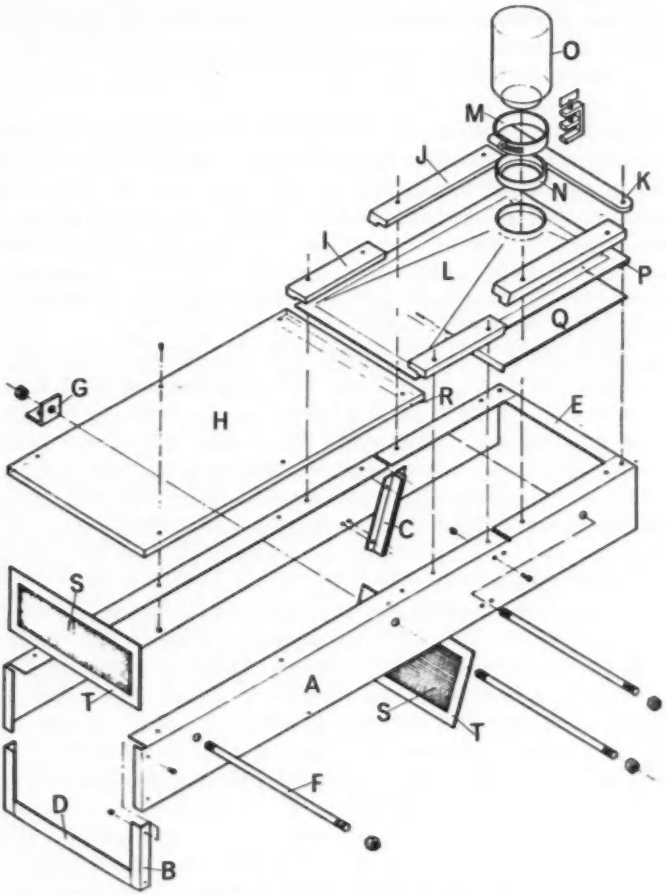

FIG. 2. Exploded isometric layout of stream emergence trap.

enclosed an area 20 × 50 cm (0.1 m²) and operated satisfactorily on substrates ranging from silt to coarse gravel. They required a depth of at least 12 cm to function properly.

The traps were set funnel end downstream, forced about 2 cm into the substrate, and secured in position with one or two stainless steel stakes. The front screen was usually left in place but occasionally it was removed to convert the trap into a sampler for collecting drifting insects.

As insects inside the trap leave the sediment to emerge they are carried downstream toward the funnel. The rear screen is sloped to help eliminate the possibility of pupae being held against the screen by the current. Once

inside the funnel where currents are minimal the slope of the funnel probably serves as the major impetus for directing the pupae or nymphs into the emergence jar. The jar is half filled with air and has a still water surface onto which the adults can emerge.

During this investigation the adults and their exuviae were usually removed from the trap every 2nd day. To remove a sample the jar was unscrewed while being kept under water. The mouth of the jar was then covered with one hand, the jar lifted out of the water, inverted, and capped with a numbered lid corresponding to the station number. An alternate method was to cap the jar while it was still under water. A small amount of ethanol was squirted into the jar to kill the specimens. They were then picked out with forceps and preserved in 70–75% ethanol.

The only major difficulties that were encountered occurred during a period of unusually high precipitation. This produced a spate in both streams which moved some of the traps and prevented the servicing of others. Other anticipated problems failed to develop. The screens on the trap were designed so that they could be quickly removed and replaced once they started to become clogged. However, algal growth was not of major importance and since the screens were submerged floating debris passed over them. As a result the screens as well as the rest of the trap could be kept clean by an occasional scrubbing with a brush.

In most cases the exuviae and adults collected in the traps were in good condition. This was true both when the sampler was used in the regular manner and when the front screen was removed. Chironomidae and Trichoptera were particularly numerous in the samples and they were usually collected in very good condition with the ratio of adults to pupal exuviae very nearly 1:1. Many Ephemeroptera were also collected including a large proportion of adults along with their subimagal and nymphal exuviae. Other insects were less frequent in the collections.

No detailed comparisons of the numbers of benthic larvae and emerging adults have as yet been made; however, there is some indirect evidence that the traps produce reasonably quantitative samples. Less than 25% of the more than 900 samples were empty and during periods of high emergence many of the traps collected more than 30 specimens during the 2-day sampling interval. The estimated emergence per square meter during such periods exceeded 150 per day, a reasonable value for streams located on Precambrian shield (Ide, 1940; Sprules, 1947). The empty samples that did occur can probably be attributed primarily to the phenology of the emerging insects rather than any malfunctioning of the trap.

A simple modification of this trap that would adapt it to other types of problems is to seal off the bottom. This modification means that the substrates and fauna inside the trap can be controlled and the emergence of insects from such things as stones or wood debris can be studied. It also enables one to control the number and species composition of the organisms within the sampler so that the interactions of various populations can be evaluated.

The screen size (apertures 405 μ sq) is approximately the largest mesh that would still retain essentially all the pupae of the smaller Chironomidae. A smaller mesh would reduce the risk of pupae escaping through the screen, but would also have a greater restriction on stream flow. It is assumed that the smaller chironomid larvae will be able to pass both in and out of the enclosure through the screen and in addition many organisms may move back and forth below the 2 cm that the trap penetrates the substrate. It is hoped, though not proven, that movements in and out of the trap will approximate one another.

Acknowledgments — Dr O. A. Sæther and Mr J. F. Flannagan of the Fisheries Research Board of Canada, Freshwater Institute, Winnipeg, Man., were consulted frequently during the development of this emergence trap and their suggestions are much appreciated. I would also like to thank Messrs William Burton and Allen Wiens who built the prototype trap as well as most of the later models.

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Occurrences of the Little Sculpin, *Myoxocephalus aeneus*, in Newfoundland Waters

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ENNIS, G. P. 1969. Occurrences of the little sculpin, *Myoxocephalus aeneus*, in Newfoundland waters. J. Fish. Res. Bd. Canada 26: 1689–1694.

Collections of the little sculpin, *Myoxocephalus aeneus*, in Newfoundland coastal waters during 1965–67 show that the species is much more common here than the previous records indicate. It occurs all around the island but its distribution is uneven and it appears to be more abundant on the west coast than on the east coast.

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ONE HUNDRED AND FORTY-THREE little sculpins, *Myoxocephalus aeneus* (Mitchill), were taken in 1965–67 in various places in Newfoundland coastal waters — 20 by the author while collecting the shorthorn sculpin, *M. scorpius*, for biological

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TABLE 1. Data on newly recorded specimens of *Myoxocephalus aeneus* from Newfoundland waters.

Date	Place	Total length	Sex	Maturity	Fin ray formula[a]			Depth (*ft*)	Method of capture	Bottom type
					D_1	D_2	A			
May 30, 1965	Piccadilly Port au Port Bay	13.6[b]	F	Resting; ova 0.2 mm in diam[c]	–	–	–	6	Smelt net	Muddy-sandy with eelgrass
Aug. 5, 1965	Boswarlos Port au Port Bay	7.3[b]	F	Resting; ova 0.2 mm in diam	10	14	11	30	Small lobster trap	–
July 7, 1966	Long Point Port au Port Bay	8.1	–	–	9	15	11	30	Diving	Rocky with sandy areas
Aug. 9, 1966	Two-Guts Barachois Port au Port Bay	9.4[b]	M	Resting	–	–	–	2	Oyster tray	Muddy-sandy with eelgrass
Aug. 19, 1966	" "	10.3(9.5[b])	M	Resting	9	14	11	2	Shrimp drag net	" "
" " "	" "	11.2(10.3[b])	F	Resting; ova 0.3 mm in diam	9	15	11	2	" " "	" "
" " "	" "	8.3(8.0[b])	F	Resting; ova 0.2 mm in diam	9	14	11	2	" " "	" "
Sept. 27, 1966	Freshwater Bay	12.9	F	Ripening; ova 0.5 mm in diam	9	14	12	20–50	Diving	Rocky
Sept. 27, 1966	" "	14.9	M	Ripening	9	14	11	20–50	"	"
Oct. 8, 1966	" "	15.2	M	Ripening	9	14	11	25–30	"	"
" " "	" "	16.6	F	Ripening; ova 0.6 mm in diam	10	15	12	25–30	"	"
" " "	" "	14.1	M	Ripening	9	14	11	25–30	"	"

Oct. 16, 1966	"	"	17.3	F	Ripening; ova 0.7 mm in diam	9	15	12	15–25	"	"
" " "	"	"	15.3	M	Ripening	10	14	12	15–25	"	"
" " "	"	"	15.5	F	Ripening; ova 0.7 mm in diam	10	14	11	15–25	"	"
" " "	"	"	13.7	M	Ripening	8	14	11	15–25	"	"
" " "	"	"	15.4	F	Ripening; ova 0.6 mm in diam	–	–	–	15–25	–	"
" " "	"	"	11.9	F	Ripening; ova 0.6 mm in diam	9	14	11	15–25	"	"
Nov. 12, 1967	"	"	19.4	F	Ripe; ova 1.0 mm in diam	–	–	–	30–40	"	"
Oct. 22, 1966	Bay Bulls		14.8	F	Ripening; ova 0.7 mm in diam	–	–	–	30	"	"

[a]Last two rays of soft dorsal and anal fins were separated.
[b]Length after preservation in 10% formalin (others were measurements of fresh specimens).
[c]Measurements from ovaries preserved in 10% formalin.

sampling and 123 by Dr D. E. McAllister and the late Mr W. H. Van Vliet of the National Museum of Natural Sciences, Ottawa, Ont., while on a field trip to Newfoundland. Previous records for Newfoundland waters include eight specimens collected at Piccadilly, Port au Port Bay in September 1922 (Johansen, 1926) and two specimens collected at Raleigh in July 1929 (Jeffers, 1932). Newfoundland occurrences of the little sculpin or grubby are of special interest because it is here that the species attains the northern limit of its range.

My specimens were identified mainly on the basis of fin ray formulae but differences in size at maturity and length at age between this species and the shorthorn sculpin with which it is so easily confused (Ennis, in preparation) were also useful. Data on the newly recorded specimens are given in Tables 1 and 2. In my collections the specimens from Freshwater Bay on the east coast were generally much larger than those from Port au Port Bay on the west coast. According to Bigelow and Schroeder (1953) and Leim and Scott (1966) the species rarely exceeds 6 inches (15.2 cm) in length. Half the specimens from Freshwater Bay were larger than 6 inches. The maximum size was $7\frac{3}{5}$ inches (19.4 cm) (Table 1). The largest from Port au Port Bay was about $5\frac{1}{2}$ inches (13.6 cm) in length. All the east coast specimens were collected while scuba diving but only one west coast specimen was collected in this manner; it was about half the average size of the east coast specimens.

TABLE 2. National Museum of Natural Sciences collections of *Myoxocephalus aeneus* in Newfoundland waters.

Date (*1966*)	Area	No. of specimens	Depth of capture (*ft*)	Bottom type
June 10	West Bay, Port au Port Bay	2	0–3	Sandy, some bed rock patches
11	St. Georges Bay (north side of mouth of St. Georges River)	1	0–$2\frac{1}{2}$	Gravel and sand, then sand with seaweed detritus
11	St. Georges Bay (2 miles west of Flat Bay)	2	0–$2\frac{1}{2}$	Sand
12	York Harbour Bay, Bay of Islands	1	0–3	Gravel, sand, some boulder
12	Blow-me-down, Bay of Islands	5	0–$3\frac{1}{2}$	Tide pool
12	Lark Harbour, Bay of Islands	1	0–$2\frac{1}{2}$	Gravel
15	St. Pauls Inlet (20 miles north of Bonne Bay)	1	0–1	Sand and gravel
16	$8\frac{1}{2}$ miles south of River of Ponds settlement	5	0–$3\frac{1}{2}$	Tide pools
17	St. Margarets Bay (west of Reefs Harbour)	4	0–$1\frac{1}{2}$	Tide pools
17	St. John Bay (1 mile east of Ferrolle Point)	24	0–$2\frac{1}{2}$	Tide pool
18	$12\frac{1}{2}$ miles south of Bia Brook	2	0–$\frac{1}{2}$	"
19	Squid Cove (3 miles north of Barr'd Harbour)	12	0–2	"
25	Eastport Bay (northside) Bonavista Bay	2	0–2	"
28	1 mile northeast of Port aux Basques	7	0–$1\frac{1}{2}$	Mud
28	Grand Bay East $1\frac{1}{2}$ miles northeast of Channel-Port aux Basques	54	0–2	Gravel and sand

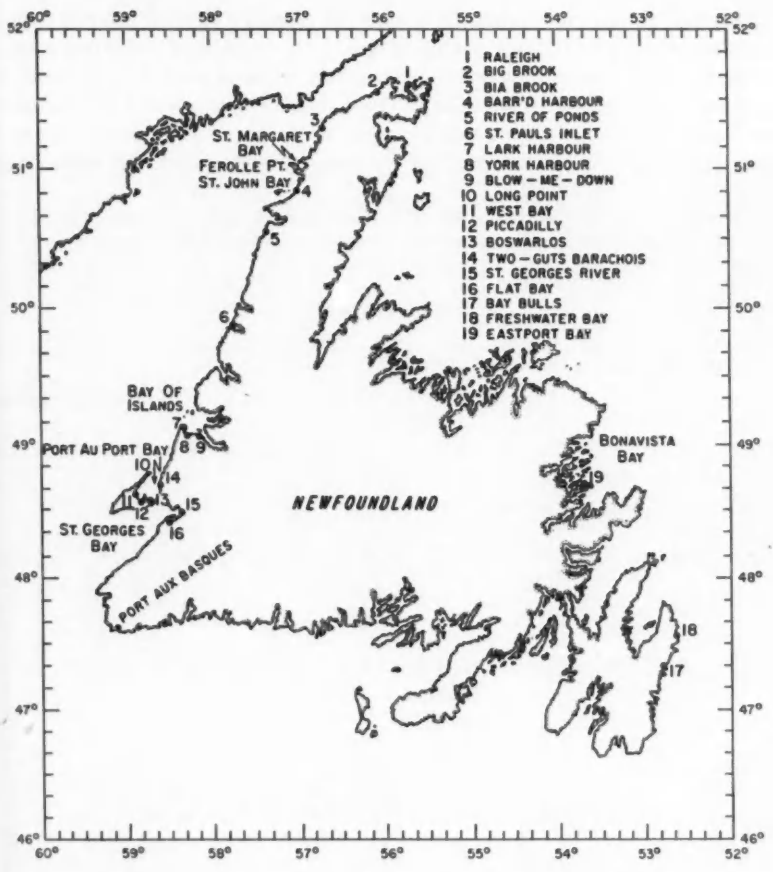

FIG. 1. Newfoundland, showing places mentioned in text and given in Tables.

The little sculpin occupies a variety of habitats in Newfoundland coastal waters including shallow (less than 3 ft) water in well-protected areas on mud, sand, and gravel bottom, in bedrock tide pools along exposed shoreline, and in relatively deep (15–50 ft) water along exposed shoreline on rocky bottom.

I collected no immature specimens. All those from the west coast were in the resting stage of maturity and those from the east coast, which were collected in autumn and early winter, were ripening (Table 1). Cox (1921) reported a ripe female taken in late June at the Magdalen Islands. Spawning probably takes place during the period late autumn to early winter; however, no egg masses were found during winter diving which was concentrated in Bay Bulls.

Although the species occurs all around the island, its distribution is uneven and, although no quantitative sampling was done, it appears to be more abundant on the west coast than on the east coast. This is probably because the west coast is generally warmer than the east coast which is under the influence of the cold Labrador Current and in view of the more temperate nature of this species it would be expected to be more abundant on the west coast.

Acknowledgments — I am grateful to Dr D. E. McAllister, National Museum of Natural Sciences, Ottawa, Ont., for confirming my identification of the specimens I sent him and for giving me his records to use in this note.

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Muscle Damage in Adult Atlantic Salmon Caught in Nylon Gillnets

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Ligation of an adult Atlantic salmon with a cord created a bruise in the epaxial muscles similar to that observed in a salmon caught by a nylon gillnet. There were no external manifestations of these lesions. Although only 10 such salmon have been observed, the incidence of this type of damage could be high because of the recent and widespread use of nylon gillnets for Atlantic salmon.

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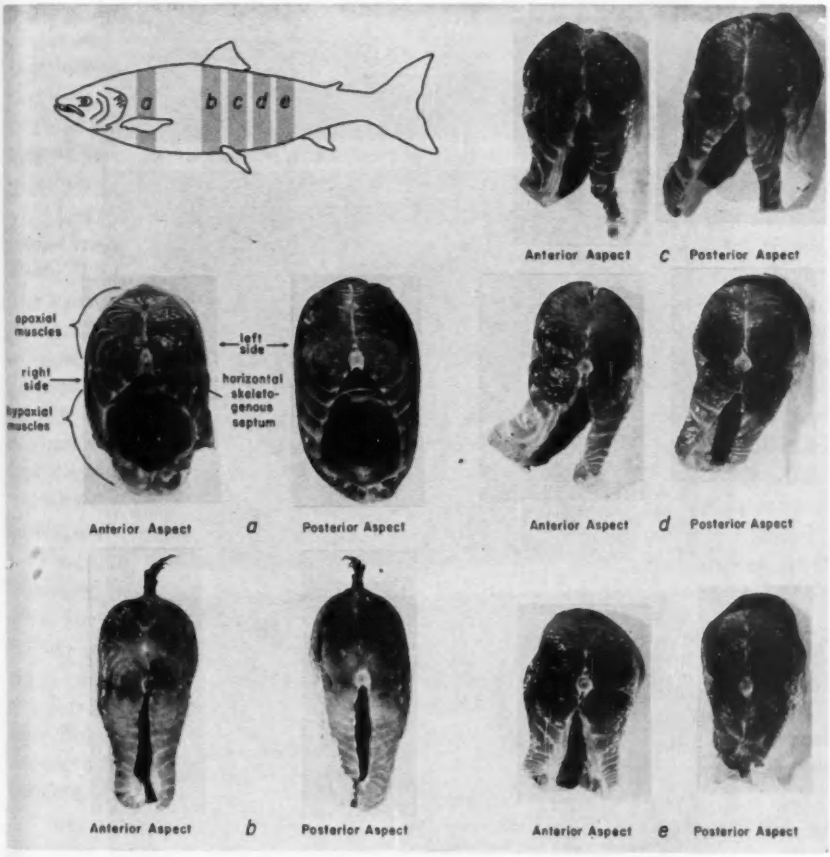

FIG. 1. Skeletal muscle lesions in Atlantic salmon steaks. The sketch indicates the positions on a salmon from which the steaks were obtained. Steak *a* is from a salmon ligated with a cord, *b* from a salmon caught in a nylon gillnet, and *c* to *e* from another salmon caught in a nylon gillnet.

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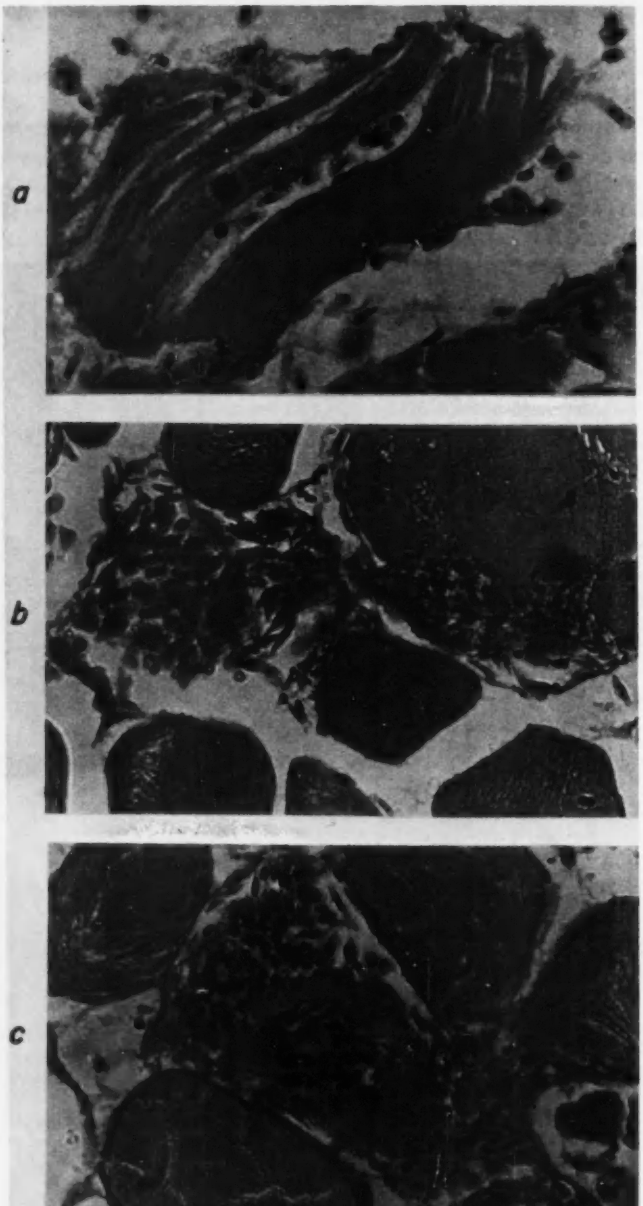

FIG. 2. *a*, A longitudinal section showing red blood corpuscles inside a skeletal muscle fibre of a salmon ligated with a cord. *b*, A cross section showing red blood corpuscles under the sarcolemma of a skeletal muscle fibre of a salmon caught in a nylon gillnet. *c*, A cross section showing a ruptured blood vessel among skeletal muscle fibres of a salmon caught in a nylon gillnet. All photomicrographs were taken at a magnification of 400×, and sections *b* and *c* are from the same salmon.

DURING JUNE AND JULY 1966, July 1967, and June 1968, cross sections of the bodies ("steaks") of 10 adult Atlantic salmon (*Salmo salar* Linnaeus) with skeletal muscle lesions were brought to the Biological Station, St. John's, Nfld., by members of the public. The salmon, eight 2-sea-year adults ("salmon") and two 1-sea-year adults (grilse), caught in gillnets along the coasts of the Avalon Peninsula, had been purchased round directly from fishermen. Each buyer stated that there were no external lesions, that the flesh felt firm, and that the fish appeared healthy when purchased; the abnormal tissues were not discovered until the fish were being prepared for cooking. The steaks were from between the head and adipose fin (Fig. 1). In some instances only one or two steaks from a salmon were brought in; in other instances several steaks were brought in so that a portion of the fish could be put back together.

Lesions were a brownish-red (color #708, Séguy, 1936) pulpy mass whereas tissue in the remainder of the steak was a normal orange (color #186, Séguy, 1936). In some instances the lesions extended through a portion of the body. For example, the lesions in steaks *c*, *d*, and *e*, in Fig. 1, which were taken from the same specimen, extended from beneath the dorsal fin back almost to the adipose fin and were mainly confined to tissue around the horizontal skeletogenous septa. In other instances the lesions occurred only in a short section of the body. The posterior portion of the steak in Fig. 1*b*, for example, had a massive lesion with all the epaxial and some of the hypaxial muscles affected but tissues in its anterior portion were relatively unaffected.

At first it was thought that the lesions were the result of infection, but protozoan parasites were not observed in smears and sections of the lesions, and salmon and brown trout parr inoculated with organisms cultured from damaged tissues of two salmon on Brain Heart Infusion Agar at the St. John's Fish Inspection Laboratory did not develop lesions.

It was then thought that the salmon could have been bruised. For example, up to one-third of Greenland halibut (*Reinhardtius hippoglossoides* (Walbaum)) caught by gillnets have discolored (pink–brown) fillets (Kamra, MS, 1967). The discoloration only occurs in the smaller fish and is caused by internal hemorrhage apparently as a result of being caught by their bodies in nylon gillnets.

On the hypothesis that the muscle lesions in salmon might be due to the same cause, a lively 2-sea-year salmon, caught in a gillnet in July 1968, was ligated with a noose of fine cord placed around the body just posterior to the head. The fish was allowed to die, and its body was severed at the constriction. The ligation had caused blood vessels in the epaxial muscles to rupture and bleed (Fig. 1*a*). Red blood corpuscles were present beneath the sarcolemma of muscle fibres in tissue taken from the ligated salmon (Fig. 2*a*) and from a salmon whose muscle lesions were suspected to have been caused by ligation in a gillnet (Fig. 2*b*). Ruptured vessels were also evident in the salmon caught in the gillnet (Fig. 2*c*).

Blood corpuscles do not occur naturally under the sarcolemma except as a result of hemorrhage. Constriction causes vessels to rupture. In the instance of the salmon in Fig. 2*b* and *c* the constriction is believed to have been that of gillnet webbing around the body. A fish so enmeshed probably struggles a great deal increasing the ligation pressure of the gillnet webbing causing the rupture of more vessels and progressively more hemorrhage.

The salmon described herein are an unknown fraction of those landed with such lesions. The incidence of such salmon could be high. Most of the lesions observed were in 2-sea-year salmon and such fish are believed to comprise most of the landings in the Avalon Peninsula area where 4½-, 5-, and 6-inch stretched-mesh nylon gillnets are used. The nylon twine may be the important factor here. Salmon caught by their bodies in such material are probably more firmly enmeshed than in gillnets of say, cotton, because nylon is a springy material which stretches under load, permitting fish to penetrate farther into the meshes. Moreover, nylon twines are tough and are able to withstand the strain placed on them by enmeshed salmon struggling to get free (Carrothers, MS, 1957). Nylon twines are also fine and can exert a great deal of pressure on a given point and it is this constrictive pressure which is presumed to rupture the blood vessels.

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